Developing more effective conservation and research

the case of the Siberian flying squirrel

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Table of contributions

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I. Also included in the doctoral dissertation of Sanna Mäkeläinen.

Contents

ABSTRACT

Research and evaluation are crucial components of evidence-based policy, decision-making and effective conservation management. As research consumes the same limited resources that could be used for conservation, it should provide as valuable and useful information as possible. This requires framing research questions to be relevant to both researchers and users of the information. A general problem is that researchers may be detached from conservation policy and practice, and thus do not recognize information needs. Furthermore, measuring and predicting effects of conservation is not an easy task. The spatial scale considered, and whether the costs and side effects are taken into account, may affect the conclusions. Effective conservation has population-level effects, but accurately measuring population change requires adequate resources and both ecological and statistical expertise. In addition, as societal actions and change in human behaviour are needed to bring about the desired changes, interdisciplinary approaches are needed for finding solutions to conservation problems.

In this thesis, I use the conservation of the Siberian flying squirrel (*Pteromys volans*) in Finland as a model case for developing more effective conservation research. As an arboreal species, the flying squirrel is threatened by forest habitat loss and degradation. I evaluate the ecological effectiveness of species protection regulation along with the side effects it has had on forest owner attitudes toward the species. I use species distribution modelling (SDM) to predict the occurrence probability of the species in Finland. I also evaluate the methods and results of the species monitoring scheme by using information from the SDM and modelled relationship between the species observed occurrence and abundance.

I found that the effectiveness of the prior approval system for forest management on flying squirrel nest sites was low but made the species a symbol of broader socio-political disputes. Conservation ineffectiveness is partly due to insufficient restrictions for forest management, but also due to lacking occurrence information. I found that species occurrence probability is explained by several environmental variables, but the ability of SDM to predict occurrence at specific sites and years remains limited with available data. I also found that the design of the population monitoring scheme does not allow reliable inference of the change in population size from the collected occurrence data.

To conclude, the effectiveness of both conservation measures and research related to the evaluation and monitoring of the effects of conservation – including the population monitoring scheme – have suffered from shortcomings. Certain relevant study questions have been ignored, the monitoring scheme suffers from methodological problems, available data are not analysed or synthetized, or results have not been provided in usable form. In addition, the connection between available information and conservation policy and practice is very weak: even the most usable and objectively relevant information may not have substantial instrumental value. Much stronger partnerships between policymakers, managers and researchers of various disciplines is needed to increase the effectiveness of conservation and conservation research.

TIIVISTELMÄ

Tutkimus ja vaikutusten arviointi ovat keskeisessä osassa tehokkaan luonnonsuojelupolitiikan ja käytännön kehittämisessä. Tutkimus kuitenkin kuluttaa samoja rajallisia resursseja joita voitaisiin käyttää suojelutyöhön – siksi sen pitäisi tuottaa mahdollisimman hyödyllistä ja käyttökelpoista tietoa. Tämä edellyttäisi, että tutkimuskysymykset ovat merkityksellisiä sekä tutkijoille että tiedon käyttäjille. Tutkijoiden yhteys luonnonsuojelun käytäntöön on kuitenkin monesti heikko, eivätkä he siksi välttämättä tunnista todellisia tiedontarpeita. Suojelun vaikutusten arvioiminen on ylipäätään vaikea tehtävä. Alue jolla vaikutuksia mitataan ja se, huomioidaanko kustannuksia ja sivuvaikutuksia, saattaa vaikuttaa johtopäätöksiin. Tehokas suojelu vaikuttaa populaatiotasolla, mutta populaatiokoon muutosten mittaaminen vaatii riittäviä resursseja ja sekä ekologista että tilastotieteellistä asiantuntemusta. Luonnonsuojeluongelmien ratkaisu vaatii muutoinkin monitieteisiä menetelmiä, koska se perustuu yhteiskuntatason toimiin ja ihmisten toiminnan muuttamiseen.

Väitöskirjassani pyrin kehittämään vaikuttavampaa luonnonsuojelubiologista tutkimusta käyttämällä esimerkkitapauksena liito-oravan (*Pteromys volans*) suojelua Suomessa. Liito-oravaa uhkaavat sille sopivien metsäelinympäristöjen määrän väheneminen ja niiden laadun heikentyminen. Väitöskirjassani arvioin lajisuojelun ekologista vaikuttavuutta sekä suojelun sivuvaikutuksia metsänomistajien asenteisiin liito-oravaa kohtaan. Tuotan habitaattimallin avulla arvion lajin paikallisesta esiintymistodennäköisyydestä Etelä- ja Keski-Suomen alueella ja arvioin esiintymismallin sekä simuloitujen populaatioiden avulla lajin seurantaohjelman menetelmien ja tulosten luotettavuutta.

Tulosten perusteella liito-oravan lajisuojelun toteutus on tehnyt lajista sosiopoliittisten erimielisyyksien symbolin, mutta suojelun ekologinen vaikuttavuus on jäänyt hyvin heikoksi. Ohjeistus lisääntymis- ja levähdyspaikkojen turvaamiseksi metsien hakkuissa ei riitä turvaamaan hakkuiden uhkaamien pesäpaikkojen ekologista toiminnallisuutta. Koska esiintymistieto on hyvin puutteellista, suurta osaa pesäpaikoista ei huomioida. Vaikka lajin paikallista esiintymistodennäköisyyttä voidaan mallintaa siihen vaikuttavien ympäristömuuttujien avulla, ennustusten tarkkuus on vaatimaton suhteessa lisääntymis- ja levähdyspaikkojen suojelukäytäntöön, joka edellyttää tietoa käytössä olevien pesäpuiden sijainnista. En pystynyt arvioimaan luotettavasti Suomen liito-oravapopulaation muutosta lajin seurantaohjelman keräämästä aineistosta siihen liittyvien epävarmuuksien vuoksi.

Löysin kehitettävää sekä suojelukeinojen vaikuttavuudesta että suojelun vaikuttavuuden arvioinnista. Tutkimuksen suurimpia puutteita ovat se että joitain merkityksellisiä tutkimuskysymyksiä ei ole tarkastelu ollenkaan, seurantaohjelmassa on menetelmällisiä ongelmia, kaikkea saatavissa olevaa dataa ei ole hyödynnetty, kerättyä dataa ei ole analysoitu, siitä ei ole tehty yhteenvetoa tai tuloksia ei ole julkaistu käyttökelpoisessa muodossa. Lisäksi tiedon ja luonnonsuojelupolitiikan ja -käytännön välinen kytkös on tällä hetkellä hyvin heikko – edes käyttökelpoisella ja merkityksellisellä tiedolla ei välttämättä ole merkittävää instrumentaalista arvoa. Tutkimuksen ja luonnonsuojelun vaikuttavuuden lisääminen edellyttäisi huomattavasti nykyistä tiiviimpää yhteistyötä päätöksentekijöiden, virkamiesten ja eri alojen tutkijoiden välillä.

SUMMARY

1. INTRODUCTION

An ever-growing amount of information is available concerning biodiversity, its value to humans (Cardinale et al. 2012), and the fact that biodiversity is being lost in the sixth mass extinction due to human actions (Ceballos et al. 2017). As a result, we have reached a global agreement to protect biodiversity (CBD 2012).

When a species becomes endangered, the expected course of collective policy response is to protect it through international treaties and national legislation (Epstein 2006). But endangered species are just the tip of the iceberg: populations of many other species are also declining (Hughes, Daily and Ehrlich 1997, Ceballos et al. 2017). This decline of populations indicates more profound changes in ecosystems than the extinctions of rare species. From this perspective, certain positive steps have been taken during recent decades: e.g. European Union member states have agreed to take measures to reach or maintain the favourable conservation status (FCS) of a wide range of species and habitats (92/43/EEC, 2009/147/EC). The definition of FCS requires not only that the species itself is viable, but that it also maintains itself in the long term as a viable component of its natural habitats (see Mehtälä and Vuorisalo 2007, Epstein 2016).

However, despite a huge amount of ecological knowledge and international agreements claiming biodiversity should be protected, we have failed to halt species losses and population declines (Butchart et al. 2010, Ceballos et al. 2017). A gap between conservation science and the policy and actions we are implementing is widely recognized (Knight et al. 2008): in many cases we already know what the problem is – we are just not fixing it. The crucial question for all conservation scientists is: what can we do to help narrow this gap?

1.1 Impact of information

Research plays a role in whether and how society observes conservation problems and how general conservation goals and more specific objectives are formulated (see Figure 1). Research also affects our ability to solve the problems we believe to be important. Science can be applied both for informal policy processes and science engagement that guide natural resource management and conservation and for the implementation or revision of legislation and operational policies (Moore et al. 2018). To understand and evaluate how research affects all levels of policy and decision-making from international policymaking and legal reforms to small-scale management and decisions of individuals, we should consider who is using the information, the process of information use and the various ways information can be used.

The question of agency is at the core of the gap between available information and actions: who has the responsibility, right and capacity to act as a response to information, who sets the goals and what actions are they taking (Mermet et al. 2013)? The type of conservation research considered relevant depends on who we believe is going to use the information and how. For example, if scientists wish to see their research applied to legal reforms, they should be aware at which levels of government their research subject is regulated and which legal processes are involved (Moore et al. 2018). Conservation scientists tend to believe that information creates political will to act and should, thereby, be converted by governments into appropriate laws and regulations, including economic and other policy instruments. Thus, our implicit assumption is that conducting good science will lead to better environmental policy and decision-making and, therefore, will help achieve conservation goals. Under this "government paradigm" on collective action, the relevance of conservation research depends on whether researchers provide convincing and solid advice for the use of authorities: e.g. reference goals, indicators and an objective choice of tools (Mermet et al. 2013). Actionable science and monitoring are examples of various activities for linking science to environmental decision-making (see Moore et al. 2018). Actionable science refers to science that informs or guides decisions in the management of natural resources and often targets a specific knowledge gap in a so-called "policy window" in a policy cycle (Beier et al. 2017, Rose et al. 2017, Moore et al. 2018). When considering policymaking, the process of information use could be simplified into a four-stage pathway: 1) usability of information, 2) use of information, 3) influence of information during policy processes and 4) impact of information on policy outcomes (Bauler 2012). Stages 1–3 are prerequisites for stage 4 but do not guarantee it, as information can be used in various ways. Investigators looking at the influence of evaluations on policy decisions have noted three main uses of information: instrumental, conceptual or enlightenment and political or symbolic use (see Weiss et al. 2005). Instrumental use of information happens when research provides direction to policy, and new research findings lead to a change in action. Science can e.g. inform the formulation of standards and guidelines that are incorporated in governmental laws and policies (Moose et al. 2018). This type of information use is usually limited to issues with a high degree of technicality but small societal and political impact (Weiss et al. 2005). Conceptual use refers to delayed and indirect research usage: research provides or helps form new ideas and concepts, which over time contribute to 'common knowledge' rather than directly at any one specific policy decision. Political or symbolical use refers to cases where research is used to support or justify pre-existing preferences or actions – or to delay in implementing actions (Weiss et al. 2005, Nichols and Williams 2006). A fourth type of information use is also suggested: pressure from outside may lead to imposed use of information (Weiss et al. 2005). An example of imposed use could be a case where a government will not provide funding to some conservation programme unless the programme uses measures that have been proven effective.

Lack of information may, indeed, lead to costly (Field et al. 2004) or even irreparable errors. However, although information and examination of evidence are needed to reach logical decisions, decision-making is influenced by two parallel processing systems: the cognitive analytical system and the affective system (see e.g. Weber 2006, Carmi et al. 2015). Information is important only if it arouses emotion and if the individual assimilates and internalizes it (Carmi et al. 2015). For example, emotional reactions may be limited by the gradual (rather than dramatic) nature of changes and the complexity and non-personality of the problems (Kollmuss and Agyeman 2002, Weber 2006). On the other hand, problems related to strong emotional reactions also exist: if information causes unpleasant emotions, or demands undesired action, it may be dismissed or avoided (Sweeny et al. 2010). Denial and dismissal of information are, indeed, part of many environmental conflicts (e.g. Opotow and Weiss 2000, Leviston and Walker 2012, Hiedanpää and Bromley 2013). Thus, although no one doubts that good information can lead to better decisions, this may not happen for many reasons. Lack of public, political and economic support for implementing recommendations delivered by conservation scientist may be the main barrier for implementing needed actions (Rose et al. 2018): without public and political support positive decisions concerning conservation are not made. As goals and decisions on how to behave or invest common resources are always based on the value judgments of the community in interest, successful conservation policies are based not only on sound ecological understanding and effective practices, but they are also economically feasible and socially acceptable. To become influential, and therefore to have an impact, information must be perceived by the actors as legitimate, credible and salient (Cash et al. 2003, Bauler 2012, Cook et al. 2013). Conservation scientists have recognized that human dimensions must be integrated with conservation and environmental management to achieve the best outcomes (Bennett et al. 2017). However, most conservation studies are still monodisciplinary and follow traditions of either ecological or sociological research. This is unfortunate, as ecological studies can be myopic and ignore economic and social constrains and thus produce recommendations that lack applicability, while sociological studies focusing on human perceptions ignore ecological effectiveness.

1.2 Monitoring and evaluation schemes in conservation

Reasons and general motivation for protecting the environment, nature and species usually rises from some change that is 1) observed or predicted, 2) considered negative and 3) communicated between people (see e.g. Greenwood 2003, Dunlap 2008, Pullin et al. 2013). Sometimes changes are so rapid and profound, and causal relationships so obvious that the public and policymakers draw correct conclusions by themselves (Dunlap 2008). Many times, however, the rate of the change is so slow, the change is otherwise difficult to detect and/or the causalities so complex that scientifically planned monitoring and evaluation schemes are needed.

Monitoring can be defined as "a repeated assessment of status of some quantity, attribute, or task within a defined area over specified time period" (Thompson et al. 1998). The approach used in monitoring can be categorized according to its goal as either i) "surveillance monitoring", which is mostly guided by general curiosity or ii) "focused monitoring", which is planned to obtain information for conservation based on defined questions and is integrated into conservation practices (Nichols and Williams 2006). Monitoring and evaluation schemes can be used e.g. for basic research, accounting and certification, assessing species status and measuring the effectiveness of management actions (Stem et al. 2005, Lindenmayer and Likens 2010a, 2010b).

Conservation needs invariably outweigh conservation resources (McCarthy et al. 2012). This means that policy and decision-makers and managers should use resources prudently and prioritize the most important conservation objectives and effective actions (Pullin et al. 2004, 2013, Wätzold and Schwerdtner 2005, Ferraro et al. 2006, Naidoo et al. 2006). Evidence-based decision-making and effective management thus require information provided by monitoring and evaluation schemes (e.g. Thompson et al.1998, Lyons et al. 2008, Lindenmayer and Likens 2010a, 2010b, Magurran et al. 2010). However, although monitoring is a central tool to be used for assessing and achieving objectives, and the effectiveness and efficiency of conservation actions should be a common interest of policymakers and conservation scientists (see Rose et al. 2018), an overall lack of research relevant to the needs of policy and management still prevails (Pullin et al. 2004, Sutherland et al. 2004, Donald et al. 2007, McNie 2007, Sutherland and Freckleton 2012). This may partly be due to researchers being detached from the practical realities of conservation and information needs, but funding opportunities for applied research are also limited.

Evaluating the effectiveness of conservation actions and comparing the effects of decisions and actions may additionally be a difficult task (Pullin et al. 2013, Figure 1). For example, an effect may appear only after an extended period of time or separating the effects of simultaneous actions may not be possible. Locating control sites to estimate outcomes without an intervention may also be difficult or impossible (see Geldman et al. 2013). Even if the effects of an action are measured correctly, comparing the effects of various actions may be difficult: e.g. should a highly effective intervention on a small area be selected or a weaker intervention across a wide area? The researcher must decide where and over how large an area the effects are measured – a decision that may affect results and conclusions. Effective resource use requires the outcomes of resource allocation decisions to be monitored and evaluated in relation to the objectives of those decisions, but this is difficult if the objectives themselves are poorly formulated – as they often are.

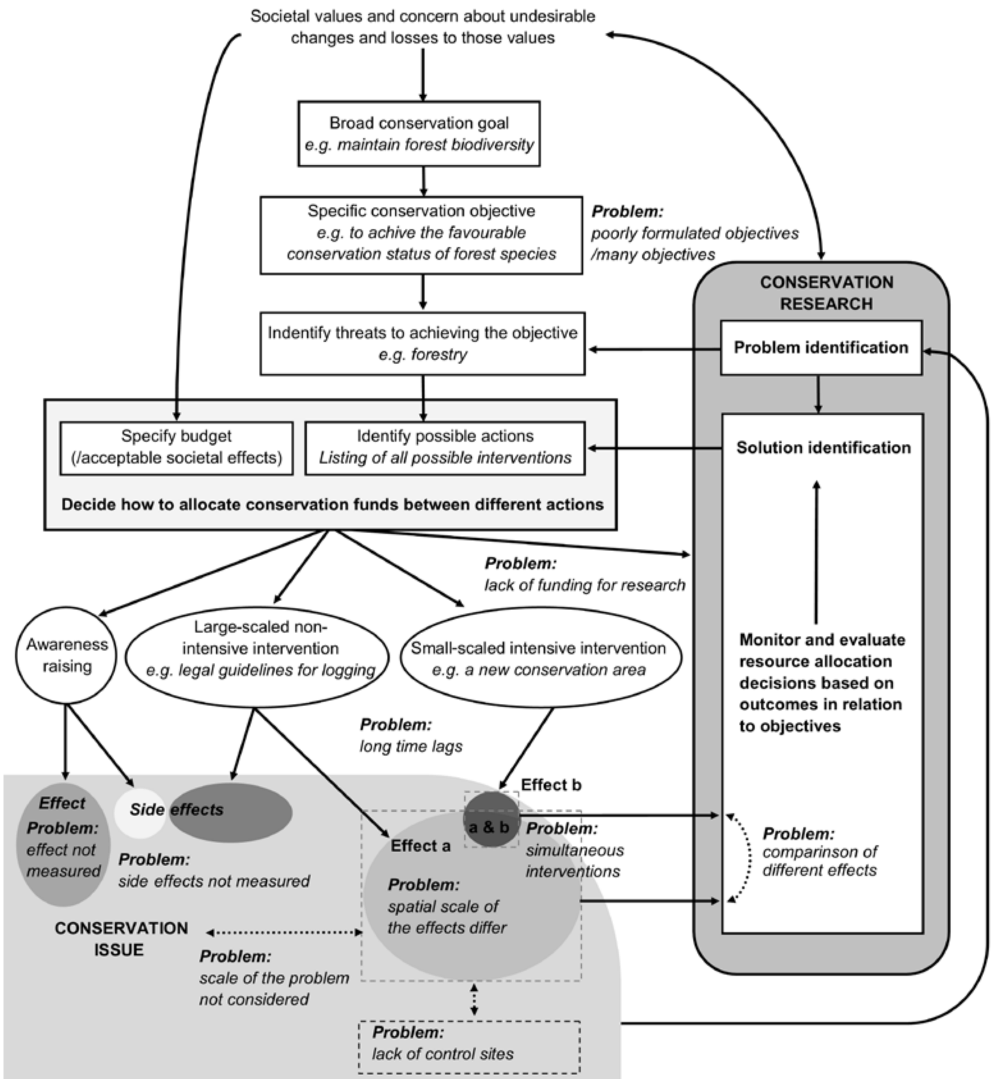

Fig. 1 *A* simplified schematic representation of the relationship between conservation research and the decision-making framework, and the problems related to monitoring and evaluation (adapted from Pullin et al. 2013).

Because of the above-mentioned reasons, information on the effectiveness of conservation actions is always incomplete, and decisions have to be made under various levels of uncertainty. As conservation resources are limited, critical consideration should be given whether to invest in monitoring or not (McDonald-Madden et al. 2010). Researchers should not gather data with only vague hope that it could somehow benefit conservation (Nichols and Williams 2006): instead, the focus should be on precise information that is needed to make conservation decisions (Nichols and Williams 2006). Thus, monitoring should not only demonstrate a decline or its reasons but also provide crucial information needed in the conservation process (Nichols and Williams 2006, Lindenmayer and Likens 2010a, 2010b). In general, the design of a monitoring programme should "follow a rational, structured process that involves a clear articulation of the purpose of the program" (Wintle et al. 2010). When planning a monitoring scheme, three fundamental questions should be carefully considered: 1) "Why to monitor?", 2) "What to monitor?" and 3) "How to monitor?" (Yoccoz et al. 2001, Jones et al. 2011, 2013).

1.2.1 Population monitoring

In population monitoring, certain population attributes (e.g. spatial distribution, abundance, density, reproduction or survival rate) for a species of interest are assessed within a defined area over more than one time unit (Thompson et al. 1998). A goal of population monitoring is to detect trends, i.e. important magnitude and direction changes in the average number of animals over a defined time period (Thompson et al. 1998). Growing demand exists for information on population trends, as this information would be a crucial part of management and conservation programmes (Thompson et al. 1998). Also, the rate of population decline may replace subjective expert-based assessments of the conservation status of species (Mace et al. 2011). However, limited funding forces researchers and agencies to prioritize which species are monitored, and only a small proportion of all species can be studied intensively enough to provide adequate data to detect changes in average numbers and spatial distributions (Thompson et al. 1998). One way to allocate limited monitoring resources is to focus on priority species defined by a risk-based approach (Regan et al. 2008). Monitoring is sometimes based on legislation or a political directive. For example, the Habitats Directive (92/43/EEC) obligates European Union (EU) member states to monitor (92/43/EEC, Article 11) and report (92/43/EEC, Article 17) the conservation status of species and habitats of 'Community interest'. The goal of such 'mandated monitoring' (Lindenmayer and Likens 2010a, 2010b) is to ensure adherence to international agreements; in the case of the Habitats Directive, monitoring is a way to ensure that the conservation status of a species is maintained at a favourable level or that it has been successfully improved with the implemented measures (see e.g. Epstein 2016, Epstein et al. 2016).

Population monitoring schemes differ greatly in the degree of potential bias in their population estimates (Thompson et al. 1998). Frequently, only data that allow very rough estimates of population trends are collected. Many existing monitoring programmes are claimed to suffer from various design deficiencies and are, therefore, inefficient use of conservation funding (Yoccoz et al. 2001, Legg and Nagy 2006, Nichols and Williams 2006, Lindenmayer and Likens 2010a, 2010b). Thus, critical evaluation of existing monitoring schemes is required.

Large-scale population monitoring programmes face two sources of variation that should be incorporated into the research design and data analysis: space and detectability (see e.g. Thompson et al. 1998, Yoccoz et al. 2001, Thompson 2012). Given that both the design and goals of monitoring are essentially statistical in nature, good design of a monitoring programme demands both strong ecological and statistical understanding. Yet, many programmes are designed with expert knowledge of the species but do not explicitly address statistical considerations (Marsh and Trenham 2008). As a result, problems with study design and data analyses are common reasons for the ineffectiveness of monitoring programmes (Caughlan and Oakley 2001, Lindenmayer and Likens 2009, 2010). In the worst case, methodological problems may lead to inaccurate interpretations of the results and to poor decision-making (Caughlan and Oakley 2001, Sheil 2001, Yoccoz et al. 2001, Field et al. 2005, Nichols and Williams 2006, Martin et al. 2007, Lindenmayer and Likens 2009, Jones et al. 2013).

Disparity between monitoring resources and the size of the area of interest is a common starting point for the study design. When an area of interest is too large to be completely surveyed, small areas must be selected for surveying in a manner that permits inference regarding the entire area of interest (Yoccoz et al. 2001, Pollock et al. 2002, Thompson 2012). Usually this requires that monitoring sites should be a random sample or a spatially stratified sample of the species distribution area or the area of interest (see e.g. Thompson et al. 1998). However, sampling units are occasionally chosen subjectively based on prior information, experience, convenience or some other criteria (Thompson et al. 1998) – and this may affect the results.

When an animal species is the subject of population monitoring, counting individuals may not be a realistic option, and certain indirect indicators, e.g. snow tracks, hair or faeces must be used instead (see e.g. Barnes 2001, Stanley and Royle 2005, Thompson et al. 2012, Latham et al. 2014). Because the relationship between individual numbers and indirect observations made of species presence often remains unclear, many monitoring schemes use so-called presence/absence or detection/non-detection monitoring methods. This means that only the number of occupied survey units is counted and the relative change in occurrence is used as a surrogate for trends in abundance (see Gaston et al. 2000, Passy 2012). However, making accurate inferences on population trend may not be possible from detection/non-detection data. Three issues have to be considered first:

i) **Abundance–occupancy relationship**. The abundance–occupancy relationship depends on several factors and may not remain constant in different situations (Gaston et al. 2000, He and Gaston 2000, Tosh et al. 2004, Joseph et al. 2006, Hui et al. 2009, Steenweg et al. 2018), but this relationship is rarely measured and verified. The relationship between occupancy and abundance is often assumed to be linear and therefore e.g. a 10% decline in occupancy corresponds to a 10% decline in animal numbers (see Gaston et al. 2000, Joseph et al. 2006, Steenweg et al. 2018).

ii) **Relationship between detection probability and animal numbers**. Researchers should estimate the probability of false absences and whether or not the number of individuals affects this probability (Gaston et al. 1999, Royle and Nichols 2003, Joseph et al. 2006).

iii) **Statistical power**. Many presence–absence monitoring schemes may not be able to detect true changes in occupancy from random noise or measure population trends accurately with the used sampling effort (Field et al. 2005, MacKenzie 2005, Rhodes et al. 2006, Ellis et al. 2014, 2015). Power analysis would indicate whether the planned scheme has feasible goals (Field et al. 2005, MacKenzie 2005, Rhodes et al. 2006, Ellis et al. 2014), yet this step is often neglected when designing schemes.

1.3 Conservation of forest biodiversity within the EU

Loss of forest area and forest biodiversity are still global environmental and conservation issues (Lindenmayer and Franklin 2002). Forests in many areas of Europe were substantially cleared by humans already during prehistoric times, or at least well before the Industrial Revolution (Kaplan et al. 2009). Although these lands have since been partly reforested (Fuchs et al. 2015), the original forest types have not been restored. The structure and composition of most of the remaining forests have also changed because of forestry.

Halting the decline of forest species has been challenging even in countries and regions that have well-developed conservation legislation and administration. Despite the Nature Directives (the Birds Directive (2009/147/EC) and the Habitats Directive (92/43/EC)) being implemented in the EU for the most part, a recent evaluation showed that the conservation status of forest habitats and species still shows no signs of improvement (European Commission 2011, 2015, 2016). Forest biodiversity continues to decline because of intensive forestry e.g. in Finland, which is one of the most forested countries of Europe and does not suffer from deforestation (Kärkkäinen et al. 2018). In Finland, ca. 600 species are known to be threatened because of forestry (Rassi et al. 2010). Furthermore, 76% of forest habitat types are classified as threatened (Kouki et al. 2018). The proportion of strictly protected forestland is less than 3% in southern and central Finland (Finnish Forest Research Institute 2011), which is not enough to protect forest biodiversity when the remaining forests are managed with current forest management methods (Virkkala and Toivonen 1999, Anonymous 2000, Hanski I. 2000, Kouki et al. 2018).

Species conservation strategies generally include three elements: species protection, site protection and conservation in the wider environment. The Nature Directives – which concern the first two elements mentioned above: species and site protection – are the principal measures for international biodiversity conservation in the EU. Biodiversity concerns are also integrated into certain other EU policies (see European Commission 2011). Individual EU states have their own laws concerning forestry and nature protection, and thus additional limitations for forestry may be in place, and species not included in the Directives may still be locally protected. Forestry is also under voluntary regulation based on forest certification programmes (e.g. Programme for the Endorsement of Forest Certification PEFC and Forest Stewardship Council FSC). Certification programmes require compliance with laws and may include additional standards for promoting ecological sustainability in forest management.

1.4 Species protection and conservation conflicts

Although species protection legislation is one of the main approaches in conservation, we often know only a little about the effectiveness and side effects of such regulation. The command-and-control approach may lead to conservation conflicts involving both disputes between groups of people about conservation but also undesirable interactions between people and the target of protection. Landowners may see command-and-control measures as a risk for their economic interests and freedoms. They may, therefore, attempt to remove the protected species or destroy protected habitats before the government places restrictions on how landowners are allowed to utilize their properties (the so-called “Shoot, Shovel and Shut Up” -method, see e.g. Brook et al. 2003, Lueck and Michael 2003, Zhang 2004, Liberg et al. 2012). Conflicts with local people have occurred frequently even when the Habitats Directive has been implemented through national legislation; for example, establishment of the Natura 2000 protected area network resulted in severe local conflicts (Hiedanpää 2002, 2013, Grodzinska-Jurczak and Cent 2011, Hiedanpää and Bromley 2011, European Commission 2016). In addition, certain protected species, such as wolves, are still under threat due to local resistance and persecution (e.g. Borgström 2012, Liberg et al. 2012, Gangaas et al. 2013, Fairbrass et al. 2016, Pohja-Mykrä 2016). Because conflicts and low acceptability of conservation may limit the effectiveness of conservation efforts (Knight 2000, Brook et al. 2003), they should be taken into consideration when selecting and developing conservation strategies and measures.

Raising awareness about protected species is one of the most common actions taken by conservationist and managers trying to decrease harmful human actions. Certain, usually charismatic, species may also be used as symbols or icons for broader conservation concerns (also called "Flagship species", Heywood 1995, Caro and O'Dotherty 1999). Once the profile of a certain species is raised, stakeholders frequently become more conscious of it and its local presence (Douglas and Verissimo 2013). This means that formerly ignored or rarely observed species can become prominent in local consciousness (Vivanco 2001). Greater awareness of a species means it may be used metaphorically as an indirect way of communicating ideas, knowledge and social experiences (Douglas and Verissimo 2013). The downside of this process is that protected species may also become symbols of incompatible goals and hostility between conflict parties. This is claimed to have happened e.g. with the spotted owl (Strix occidentalis) in the USA: for environmentalists the spotted owl became a symbol of the disappearing old-growth forests, while for loggers it symbolized threat to job security (Moore 1993). The conflict parties constructed the spotted owl in ways that were consistent with their political commitments and orientations to land management, and used it to represent and communicate their interests and agendas (Moore 1993, Douglas and Verissimo 2013). In such cases, species can be used as a political instrument for conflicting goals, and thus they are entangled in irreconcilable social conflicts (Douglas and Verissimo 2013).

1.5 Study case

In this thesis, I use conservation of the Siberian flying squirrel (*Pteromys volans*, henceforth the flying squirrel) as a model case for developing more effective conservation research. The case is interesting for several reasons. Flying squirrels are threatened by large-scale human action: forestry. The species is considered both an icon for threatened old boreal forests and an umbrella species (Hurme 2008, Selonen and Mäkeläinen 2017) and is under strict legal protection in the EU. A proportionally large amount of conservational resources has been allocated to conserving and monitoring the flying squirrel population in Finland. The level of ecological knowledge of the species is good; a review on the ecology and conservation of the species listed 51 articles written since 1982 as references (see Selonen and Mäkeläinen 2017). However, the focus of research has been on basic research while possibilities of producing policy- and practice-relevant information from existing datasets have not been fully utilized. Also, the method used for monitoring and estimating the population trend is disputed (Sulkava et al. 2008), and problems have arisen in using the monitoring data for evaluating the conservation status of the species.

Conflict and controversy have accompanied flying squirrel protection in Finland (see Haila et al. 2007). The effect that the occurrence of this strictly protected species can have on land use came as an unexpected and unpleasant surprise to many landowners, constructors and urban planners. The legal status of the species also made it possible to attempt using the flying squirrel as a tool to prevent otherwise unwanted projects or for conserving valued old forests. Finnish regional environmental authorities have had to balance between the ecological objectives of protection and the guidelines of Finnish ministries (Jokinen 2012), which do not seem to take into account the ecological information of the species (Santangeli et al. 2013b, Wistbacka et al. 2018). Natural science-inflected legal concepts that integrate EU law, national law, soft law and ecological knowledge are complex (see Epstein 2016) and leave room for various interpretations – and thus also for legal disputes.

1.5.1 Ecology of the flying squirrel

The flying squirrel is a nocturnal and arboreal rodent inhabiting Eurasian boreal forests (Shar et al. 2008, Figure 2). It is listed as 'Least Concern' in The IUCN Red List of Threatened Species but has experienced local declines or extinctions (Shar et al. 2008). In the EU, the flying squirrel is currently found only in Finland and Estonia (Timm and Kiristaja 2002). In Estonia, the species is classified as 'Endangered' (Timm and Remm 2011), but it is still widespread in Finland (Figure 3). Most Finnish flying squirrels live in commercial forests. As forestry has greatly affected both the quantity and quality of forest habitats, it is considered the main factor threatening the species (Selonen and Mäkeläinen 2017, Liukko et al. 2019). In Finland, the species favours mature forests dominated by Norway spruce (*Picea abies*) with a mixture of deciduous trees (Hanski 1998, Hanski et al. 2000a, 2001, Reunanen et al. 2002a, Santangeli et al. 2013a) – the latter of which are important both as food sources and as nest sites (Mäkelä 1996, Hanski et al. 2000b, Selonen et al. 2016, Selonen and Mäkeläinen 2017).

Fig. 2 *A* flying squirrel individual in trouble on a bicycle trail in the Helsinki city area. Flying squirrels are clumsy on the ground and therefore avoid open areas. Fortunately, the landscape in Finland is forest-dominated, and individuals can reach most habitat fragments in the landscape by gliding (Selonen and Hanski 2012). As this individual was encountered at the end of August, it may be a young dispersing individual. Picture © Elina Numminen

Adult flying squirrels are site-faithful. Females are territorial, but male home ranges overlap with both females and other males. Home range size averages 60 hectares for males and 8 hectares for females (100% minimum convex polygon for radio-tracked individuals, Hanski et al. 2000a, 2001). Species' home ranges typically consist of small-sized core areas where individuals spend most of their time (Hanski 1998). One individual usually has several nest sites, which can be tree cavities, nest-boxes or dreys (Hanski et al. 2000a, Selonen and Mäkeläinen 2017).

The species has a polygynous-promiscuous mating system (Selonen et al. 2013). Females have one to two litters during the breeding season in April–June. Litter size is usually 2–4 offspring. Almost all juvenile females and most juvenile males disperse from their natal home ranges (Hanski and Selonen 2009, Selonen and Wistbacka 2017). The life expectancy for individuals is relatively short: reported values for annual adult survival ranges from 0.43 to 0.76 (Lampila et al. 2009, Mäkeläinen 2016, Brommer et al. 2017).

1.5.2 Surveillance of conservation status and strict protection of the flying squirrel in Finland

The flying squirrel is included in Annexes II and IV(a) of the strictly protected species of the Habitats Directive (92/43/EEC). The Directive was implemented in Finland in 1997, mainly using the Finnish Nature Conservation Act (1096/1996). In this thesis, I evaluated the effects of two specific requirements of the Directive: surveillance of the conservation status and the ban on deteriorating or destroying the breeding sites or resting places of the species.

Article 11 of the Habitats Directive obligates EU member states to monitor the conservation status of species (and habitats) of Community interest. As several studies indicated a continuous population decline of flying squirrels from the 1940s (Hokkanen et al. 1982, Hanski et al. 2001, Selonen et al. 2010a, Liukko et al. 2016, 2019), the Finnish Ministry of Environment financed an extensive systematic survey of the species in 2003–2005 and following the population monitoring scheme.

Article 12(1) of the Directive obligates Member States to establish a system of strict protection for over 300 (non-avian) animal species listed in Annex IV (a) in their natural range, and prohibits:

a) *all forms of deliberate capture or killing of specimens of these species in the wild;*
b) *deliberate disturbance of these species, particularly during the period of breeding, rearing, hibernation and migration;*
c) *deliberate destruction or taking of eggs from the wild;*
d) *deterioration or destruction of breeding sites or resting places.*

For flying squirrel conservation, prohibiting the deterioration or destruction of breeding sites and resting places (Nature Conservation Act 1096/1996, 49.1§) is the most relevant of the four prohibitions of Article 12(1). Finland enacted a special 'prior approval' procedure for safeguarding the breeding sites and resting places and preventing legal consequences for forest owners and operators in 2004. According to the Finnish Forest Act (1093/1996), a forest owner or holder of felling rights has to send a "forest use declaration" to regional forest authorities (The Finnish Forest Centre) before any commercial forest felling. Regional environmental agencies (Centres for Economic Development, Transport and the Environment, ELY Centres) uphold a register of flying squirrel observations and share this information with the Forestry Centre, which supervises implantation of the Forest Act. If a forest use declaration concerns a site with previous known flying squirrel occupancy, the Forestry Centre notifies the regional environmental agency, forest owner and the holder of the felling rights. The Finnish Nature Conservation Act (1096/1996, 72 §) required the environmental agency to make a formal decision on the location of the breeding site or resting place of the flying squirrel and the permitted management of the forest. Due to a change in the Nature Conservation Act in 1 April 2016, this procedure no longer exists (see Anonymous 2015a). Instead of routine primary control, regional environmental agencies mostly provide advice and conduct ex-post supervision (Anonymous 2015a, see also Vuorinen 2017).

The fundamental question with the practical implementation of provision 12(1)d is how "breeding sites" and "resting places" and the "deterioration" and "destruction" of these sites is defined, and what practical arrangements are in place for safeguarding the sites. Although these above-mentioned concepts are legal, and created and defined to a certain extent in the law, they can only be understood by reference to ecological concepts such as species' spatial behaviour and habitat suitability. The aim of the Habitats Directive is to safeguard the "ecological functionality" of the breeding sites and resting places (Anonymous 2007). These sites should, therefore: "…continue to provide all that is required for a specific animal to rest or to breed successfully" (Anonymous 2007). However, ecological determinations still require some legal interpretation or policy judgment (see Epstein 2016).

Two soft-law documents have been directed at Finnish forest and environmental agencies, forest owners and forestry operators to advise them on the interpretation of legal concepts. The first guidelines released by the Finnish Ministry of Environment and the Ministry of Agriculture and Forestry in particular have had a significant effect on the practice of defining and safeguarding the breeding sites and resting places of the flying squirrel. This document defined the sites as small-sized: a zone with a radius of 10–15 m was required to be left intact at a documented nest site (Anonymous 2004). If the breeding site and resting place were not adjacent to the remaining forest, guidelines required leaving a corridor of trees connecting the nest site to the forest outside the cutting area. New advisory material was published in 2016, which does not present any radius for breeding sites or resting places, but instead states that: "The purpose of the Nature Conservation Act has not been to extend the definition of breeding sites or resting places to very wide areas. The law does not e.g. oblige protection of the whole flying squirrel habitat"……"Breeding site and resting place means the nest tree and those trees in the immediate neighbourhood of the nest tree that are important for the species for feeding, storing food or for protection" (Anonymous 2016, translations by the author). In addition, corridors of trees have to be preserved (Anonymous 2016).

The multijurisdictional (EU and national) nature of environmental law and science-law interface are complex. As law concepts and principles have both ambiguous (natural scientific) factual and (legal scientific) normative aspects, it may be preferable for conservation scientists to restrict themselves from trying to make legal judgements based on their own ecological results (Moore et al. 2018). Therefore, in this thesis I focus on implemented actions and their measurable effects, especially ecological effectiveness; I leave it to legal experts to evaluate whether the practice created by the above guidelines is fully compatible with the Nature Conservation Act and whether the Nature conservation Act is compatible with EU law (see e.g. KHO 2010/2840, Halonen 2014, see also Vuorinen 2017).

1.6 Aims of the thesis

My general aim in this thesis is to increase the effectiveness of research by producing information relevant for conservation policy and practice. My evaluation of the impact or protection regulation and regulation policy is outcome-based: I use both attributional (ecological functionality of breeding sites and resting places) and non-attributional (population trend) indicators for both goals concerning protection (safeguarding the ecological functionality of breeding sites and resting places and achieving favourable conservation status for the species) and for other values (side effects, resources used) (see Coglianese 2012). Policymakers, legal experts and managers may use the results for making informed decisions on how to develop conservation and the legal protection of this species.

I and **II**

In chapters **I** and **II**, I study the effects of the primary control procedure that was used to implement the ban on deteriorating or destroying species breeding sites and resting places. In chapter **I**, I estimate the direct ecological effects of the primary control procedure. In chapter **II**, I study unwanted side effects of legal protection. I examine which factors explain forest owners' attitudes toward the flying squirrel and estimate the risk of various forms of noncompliance with the law. Results of these studies can be used to develop evidence-based and effective conservation practice and policy.

III

In chapter **III**, I study factors affecting the occurrence probability of the species and predict species occurrence in central and southern Finland. Results of the study can be used to target surveys and protection measures along with population estimation and monitoring. My results can also be used to develop effective conservation strategies for the species.

IV

In chapter **IV**, I use an individual-based simulation to estimate the relationship between occupancy and abundance and to evaluate the species monitoring scheme. This information is needed for inferring population trends from occurrence data, and it can be used for revising former population size estimates.

In the Results and Discussion section, I evaluate the methods and results of the species monitoring scheme. This information can be used both in developing the monitoring scheme and in the conservation status classification of the species.

2. MATERIAL AND METHODS

2.1 Study area

All studies were performed in southern and central Finland between 59.96°N, 21.20°E and 64.13°N, 31.50°E (Figure 3). Landscapes in the area consist mainly of fine-grained mosaics of different-aged forests (Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and birches *Betula* spp. are major tree species in this area), agricultural areas, water bodies and mires. The area includes six forest vegetation zones, which differ in their climate and soil characteristics (Figure 4). Winters are relatively mild in the southern and western regions because of the lower latitudes and proximity to the Baltic Sea coast. A favourable climate and soil explain why agricultural areas are most abundant in these areas. Soil is less fertile in northern regions (Ostrobothnia, North Karelia and Kainuu) than in the central and southern regions; northern forests are therefore mostly dominated by pine. Lakes are most abundant in central and eastern regions.

The great majority of the forests in the study area are managed for timber production: most stands are thinned two or three times and clear-cut when they mature at an age of 60–90 years. Sixty to ninety per cent of the forests in this area are privately owned (Finnish Forest Research Institute 2012, 2014). Private forestry has a key role in Finland: 80% of Finnish wood used by the forest industry comes from privately owned forests (Finnish Forest Research Institute 2009). However, the average size of private forest estates is only 30 hectares, and fewer than one in five forest owners is a full-time forestry entrepreneur (Hänninen et al. 2011).

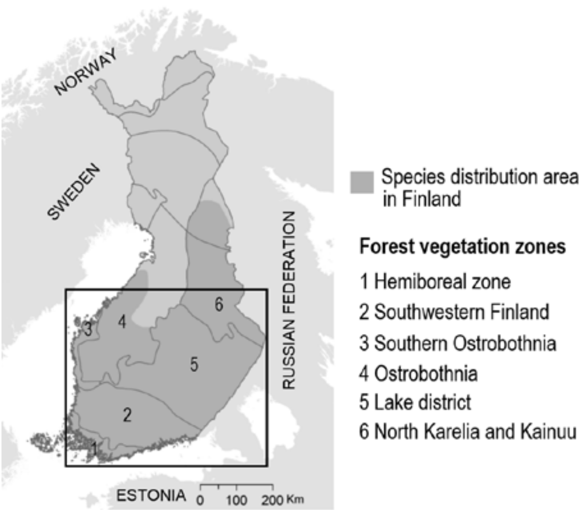

Fig. 3
Study area and species distribution in Finland. All studies were carried out in the area delimited by the black rectangle. The darker grey area represents the species' distribution area in Finland. Borders of forest vegetation zones are shown with dark grey lines.

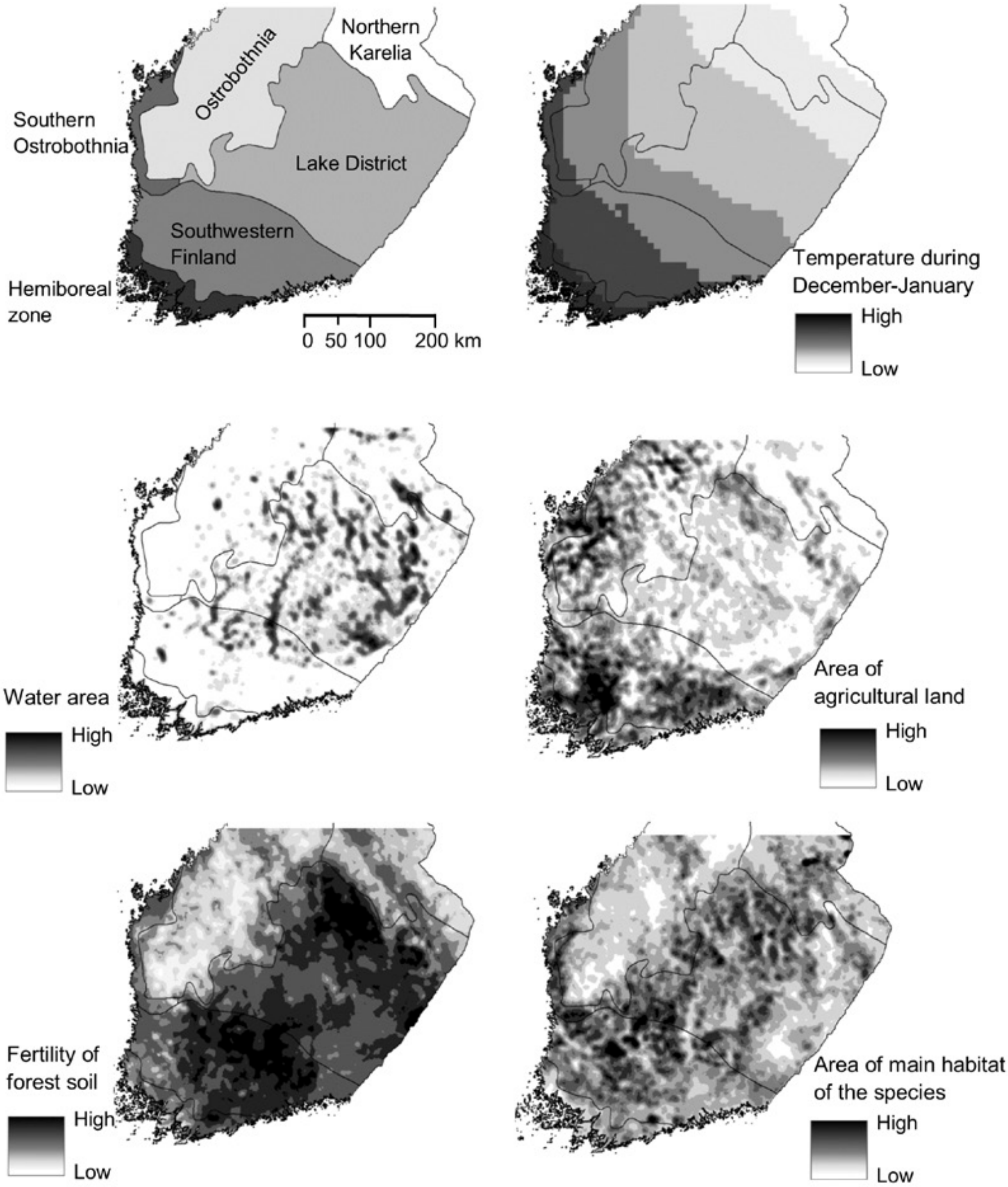

Fig. 4 Relative landscape-level differences of certain environmental variables relevant for flying squirrels in the study area. The species main habitat is defined as forest that is at least 80 years old and where the volume of Scots pine (Pinus sylvestris) does not exceed 66%.

2.2 Data collection

Data for studies **I** and **II** were collected while ELY Centres were still making decisions concerning the locations of flying squirrel breeding sites and resting places and on permitted forest management practices at those sites.

2.3 Occurrence data

In all analyses using information on species occurrence, the presence or absence of the species was defined according to the presence of faecal droppings. This is the standard method in flying squirrel surveys, as while flying squirrels are difficult observe, pellets are easily detectable and identifiable during spring and early summer (e.g. Reunanen et al. 2002a, 2002b, Hanski 2006, Santangeli et al. 2013a).

In Study **I,** I used comprehensive pellet survey data from six landscapes from surveys performed by Marko Nieminen, Marko Schrader, Jaakko Vähämäki, Ari Jokinen, Ilkka Holmila and Marita Palokoski. In addition, I surveyed a total of 100 defined breeding sites and resting places from 11 May 2011 to 4 July 2011. I obtained information on authority decisions from the case management system of the environmental authority and from the archives of the Finnish Environmental Institute SYKE.

In Studies **III** and **IV,** I used two detection/non-detection datasets provided by the Finnish Museum of Natural History: national flying squirrel survey and species monitoring data. An extensive systematic survey for the species was performed within the study area during springs and early summers of 2003–2005 (see Figure 5b, Hanski 2006, Santangeli et al. 2013a). The survey sampling was performed as follows: 1) the total area was divided into 10×10-km squares, 2) every second square was selected, 3) 10 survey sites were placed randomly on each of these selected squares. Surveyed sites were located on mineral soil and were at least one km apart. Site size, i.e. 300×300 m (9 ha), was selected to match the average female home range (8.3 ha, Hanski et al. 2000b).

After the survey, a total of 1121 survey sites from the national flying squirrel survey sites were included in the monitoring scheme using a subjective selection method. Selected sites were located in 13 regions for convenience; the regions were distributed over the species' main distribution area (Hanski 2006, Figure 5d). Prior information on species occurrence during the survey was used to define regions so that both occupied and unoccupied sites and high- and low-density areas were included in the scheme (Hanski 2006). All original survey sites within the monitoring regions (defined as 100% convex polygons including all monitored plots) were not included in the monitoring scheme. Certain sites considered unsuitable for the species were apparently left out or prior occurrence information was used in selecting the monitoring sites. The total number of monitoring sites varies between the regions (n=50–102). All regions and sites visited in 2006 have not been surveyed each year. Certain regions have been skipped completely during some years due to funding limitations. In addition, fieldworkers have skipped individual sites when they have interpreted that the monitoring plot did not include a flying squirrel habitat (see Table 1). None of the monitoring sites were surveyed in 2010–2013.

For a conservation status assessment in 2015, the population trend for flying squirrels was estimated by calculating mean occupancy during 2006 and 2007 (28.6%) and comparing that to the mean occupancy during 2014 and 2015 (22.1%) in eight regions and 632 monitoring plots (out of 13 regions and 1121 plots) (Liukko et al. 2016). Three high-occurrence regions had no data for all the years, and this seems to have affected the estimate. To form a conservation status assessment for 2019, we calculated the change in occupancy during a 10-year period in two ways: i) comparing years 2008 and 2017 and i) comparing mean occurrence in 2007–2008 and 2016–2017. Data from 749 plots were used for this, and they indicated declines of 42.3% and

36.9%, respectively (Liukko et al. 2019). The observed proportional decrease in occurrence was interpreted as a 22.7% decline in population during the 10-year period in the 2015 assessment (Liukko et al. 2016) and at least a 36.9% decline in the 2019 assessment (Liukko et al. 2019).

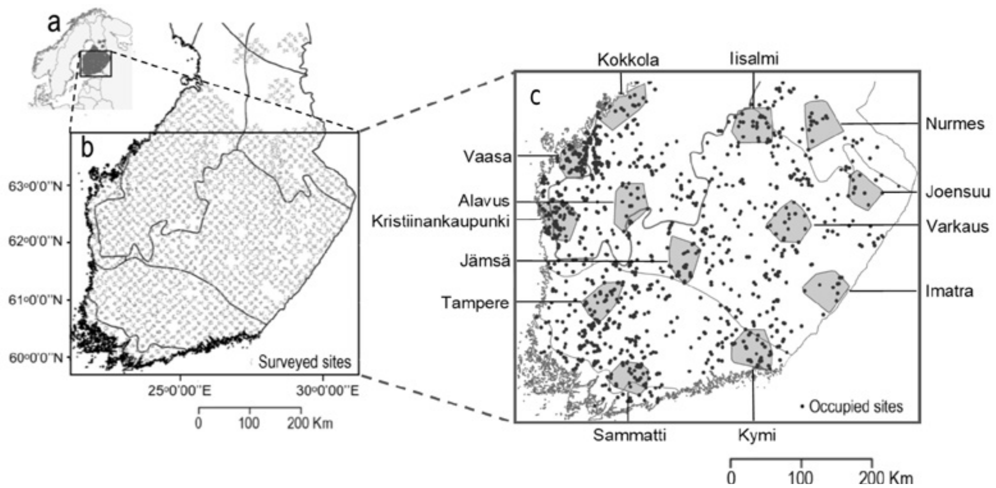

Fig. 5 a) Location of the study area, b) surveyed sites (in the study area n=9256), c) occupied sites in the study area (n=1020), d) locations of survey plots of the national flying squirrel survey (grey dots) and 13 monitoring regions (polygons). The conservation status of the species was classified in 2015 according to the monitoring data from eight regions marked in dark grey. Six vegetation zones (delimited with lines) overlap the study area.

Tab. 1 Yearly numbers of i) occupied sites ii) surveyed monitoring sites, iii) sites not surveyed because site was considered uninhabitable, iv) sites not visited that year.

Year	2003–2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Occupied	338	320	292	286	208	-	-	-	-	229	155	192	176	158
Surveyed		1121	853	794	539	0	0	0	0	1001	484	771	762	
No habitat		-	268	327	312	-	-	-	-	120	159	293	192	
Not evaluated		0	0	0	270	1121	1121	1121	1121	0	478	57		

2.4 Environmental data

Landcover maps used in this thesis were produced using spatial information from various sources. In Study **I,** I used aerial photographs and field observations to detect changes and classify habitats at breeding sites and resting places. In simulations of the six landscapes and in Studies **III** and **IV**, I used National Multisource National Forest Inventory data (MS-NFI). MS-NFI data (Tomppo et al. 2008) are based on an integration of Landsat satellite image information and ground-truthed plots. The data were provided by Natural Resource Institute Finland LUKE (http://kartta.luke.fi/opendata/valinta.html). These data contain various variables on several raster layers with a pixel resolution of 25×25 m or 16×16 m (for 2005 and 2013, respectively). I used the data for total growing stock volume, volume of pine, stand age and site fertility index. In studies **III** and **IV,** I also used information on annual forest loss, topographic data, land cover data and weather data (in study **III**). Annual forest loss data are provided by Hansen et al. (2013;

https://earthenginepartners.appspot.com/science-2013-global-forest). We obtained weather information from the Finnish Meteorological Institute FMI (https://ilmatieteenlaitos.fi/avoin-data) on a 10×10-km raster grid. For land cover information, I used CORINE land cover map data (https://land.copernicus.eu/pan-european/corine-land-cover). Topographic maps are provided by the National Land Survey of Finland NLS (https://tiedostopalvelu.maanmittauslaitos.fi/tp/kartta)

2.5 Attitude data

For Study **II**, we carried out a telephone interview survey for private forest owners between 1 June 2014 and 15 May 2015. Information of forest owners with personal experiences with flying squirrels was obtained from the case management system of the environmental authority. As a control group, we used forest owners who had not experienced protection procedures. Contact information for these forest owners was randomly drawn from the register of the Central Union of Agricultural Producers, MTK. Out of the contacted forest owners 81 persons with personal experience and 105 inexperienced persons were willing to participate the study. In order to avoid biased sample, the actual subject of the study (the flying squirrel) was not mentioned at the start of the interview. I carried out a dropout analysis in order to ensure that the sample was otherwise representative (see pp. 87–90 and section Statistical analyses and simulations in p. 24). As I found that the mean size of the forest estate differed between the groups, I included it in the structural equation model.

The survey questionnaire included a series of questions and arguments concerning beliefs, opinions and attitudes along with relevant background factors. Responses to belief, opinion and attitude arguments were given on a five-step Likert scale: agree, somewhat agree, neither agree nor disagree, somewhat disagree or disagree.

2.6 Statistical data

I used statistical information for study **I**. The Ministry of the Environment had collected information on the total area of defined breeding sites and resting places (Ministry of the Environment 2012). Certain ELY Centres had also kept records on the number of their decisions. Kai Blauberg, from the Finnish Forest Centre, calculate the number of logging plans and their median size from 2005 to 2012 at our request from national forestry data.

2.7 Statistical analyses and simulations

Study I

The estimate for the number of forest felling sites that should have led to the delineation of a breeding site and resting place was based on simulated final felling and survey plots in six actual landscapes and the observed spatial distribution of faecal pellets in those landscapes. We performed a linear regression in which the fraction of occupied felling sites was explained by the fraction of occupied survey plots. As we knew the mean occupancy of the species on the survey plots (Hanski 2006), we could use the regression line to estimate the number of occupied logging sites in the landscapes.

We used logistic regression to estimate the effect of authority decisions on sites defined as breeding sites and resting places and to examine which factors explained the presence or absence of flying squirrels. We performed backwards model selection, and additionally compared alternative models using Akaike's Information Criterion (AIC) values (Burnham and Anderson 2004).

Study II

We used exploratory factor analysis EFA (SPSS: Extraction: maximum likelihood, Rotation: Varimax) to reduce the number of variables used in further analyses. We constructed three latent variables according to the EFA. Hypothesized relationships between measured background variables, latent variables and certain individual variables were tested with structural equation modelling (Bayesian estimation method, Markov chain Monte Carlo MCMC algorithm, prior distribution: uniform distribution from -3.4 X to 3.4 X). The model was trimmed by removing insignificant hypothetical paths according to 95% confidence limits to get the value of posterior predictive p as nears to 0.5 as possible.

In the dropout analysis, I compared different groups with Kruskal-Wallis, Pearson Chi-Square or Mann-Whitney U-tests.

Study III

I used MaxEnt software package (Phillips et al. 2006; 2017, http://biodiversityinformatics.amnh.org/open_source/maxent/) for species distribution modelling. MaxEnt is a presence/background modelling tool that employs the maximum entropy algorithm for modelling species distributions and estimating parsimonious effects of various landscape features on occurrence (Phillips et al. 2006, Elith et al. 2011). Having presence-absence data available, I could use surveyed sites as background points and transform MaxEnt's raw output into estimates of occupancy probability (see Guillera-Arroita et al. 2014).

I evaluated model performance using Area Under the Curve (AUC) statistics of the receiver operating characteristic (ROC) plot. To gain further knowledge on model fit and performance, we assessed the predicted probabilities of occupancy separately for the true locations of presence and absence in the data.

Study IV

We made a spatially explicit individual-based simulation that utilizes ecological information on the species. The results (spatial distributions of individuals of different population sizes) were used for virtual surveys with the plots included in the species monitoring scheme.

3. RESULTS AND DISCUSSION

The starting point for my thesis was to produce information relevant and in useful form for developing species conservation. I have done this using approaches suggested by Mermet et al. (2013): by reflecting on the accessibility and relevance of my research and collaborating with conservation practitioners and social scientists. Although I found this approach possible and fruitful, it is suboptimal for most academic researchers. The structure of my thesis demonstrates one of the many challenges for conservation researchers: many monitoring schemes do not produce data that pass scientific peer-review (Lindenmayer and Likens 2010b). Evaluation of the monitoring scheme takes a large part of the summary, but I cannot use the results of manuscript **IV** for inferring population decline from monitoring data.

3.1 Ecological effectiveness of safeguarding breeding sites and resting places

Inadequate information of sites where species occur is a general problem for species conservation (Rondinini et al. 2006). Information of flying squirrel occurrence sets the upper limit for how effective preserving known breeding sites and resting places can be. As collecting information on species occurrence at felling sites was not possible, we instead used a simulation approach for estimating the proportion of known nest sites. According to our estimate, logging restrictions were only set in 2.7% (1.6–9.5%) of the cases in which the species was present at a felling site (**I**).

To measure the effect of a specific conservation action, we should also measure what happens without the intervention, as all positive outcomes may not be a result of the intervention (Pullin and Knight 2001). However, using true control to estimate what would have happened without the conservation intervention is difficult or impossible for many conservation studies (Pullin et al. 2013). My option was to test how forest composition affects species' persistence at breeding sites and resting places. I found that the likelihood of flying squirrel persistence depends on the current quantity of suitable, semi-suitable and unsuitable habitat around the defined breeding site and resting place (**I**). Any clear-felling appears to potentially impair the ecological functionality of a specific site. I found that if the area of suitable habitat within a 150-m radius is maintained at over 3.5 ha, the species should be able to continue its occupancy on the site with at least a 50% probability (**I**).

Other researchers have used different approaches for solving the problem of having no control group. Santangeli et al. (2013b) used before-after control-impact design, where control sites included nest sites that were left "essentially un-cut". Although such a study design is suitable for showing whether breeding sites and resting places have deteriorated despite logging restrictions, it cannot be used e.g. for defining thresholds for habitat area or for clear-cuts. Furthermore, if sites are selected subjectively, the study design can lead to a biased conclusion of the species general ability to cope with forest felling. The data of Santangeli et al. (2013b) showed that the species persisted in only 26% of breeding sites and resting places, which seems to be explained by extreme study cases (**I**). I found some faecal pellets from 61% of study sites (**I**). The current practice may not have a substantial positive effect on known nest sites, as suitable habitat outside the delimited breeding site and resting place may explain species persistence (**I**, Jokinen, 2012). When I used data from the species monitoring scheme (Hanski

2006) to calculate how large a proportion of the monitoring plots occupied in 2006 were classified as unoccupied three years later (in 2009), I came to a very similar result: the species occurred on 64% of sites occupied in 2006.

Study **I** and the study by Santangeli et al. (2013b) have a common shortcoming: species occurrence does not prove that the ecological functionality of the site remains undeteriorated. Wistbacka et al. (2018) approached the question of relationship between habitat area and ecological functionality by testing how habitat area affects the occurrence probability of breeding females. In their study, Wistbacka et al. (2018) observed that the occurrence probability of females achieved a maximum of circa 0.9 well before the habitat area of 3.5 ha when the area was calculated within a 100-m radius. However, the occurrence probability of breeding females increases significantly until the habitat area is around 10 ha when calculated within a 200-m radius. As the size of female territories is mostly smaller than 10 ha, this result implies that the probability of having close neighbours may positively affect the probability of a certain site being occupied by a breeding female. Our simulation results point to the same conclusion (**IV**).

As in most cases, the defined breeding site and resting place are very small (less than 0.3 ha; see Jokinen 2012), there is disparity between the species' home range requirements and guidelines for safeguarding nest sites (see Halonen 2014, Vuorinen 2017). Generally, establishing the scientific foundation for guidelines may be challenging because there are no clearly definable ecological thresholds for setting regulatory thresholds (Huggett 2005, Hunter et al. 2009, Vuorinen 2017). Scientific information must be translated into regulatory thresholds based on societal value judgments with respect to acceptable risk levels.

However, the main problem for this conservation strategy is that environmental agencies are unable to uphold a sufficiently comprehensive and up-to-date register of breeding and resting sites for the species. The system of strict protection presupposes the adoption of "coherent, coordinated and effective measures of a preventive nature that are supported by an adequate enforcement mechanism" (Anonymous 2007). Thus, a simple prohibition in a legal text should not be considered enough for safeguarding breeding sites and resting places. However, many EU member states have had problems with implementing the Nature directives because of inadequate funding that limits the capacity of administration to support and monitor actions. Imposing a comprehensive set of controls may be disproportionate when extensive forestry and agricultural activities are ongoing. In such cases, other preventative measures, e.g. planning regulations or best practice codes, could be used for safeguarding the breeding sites and resting places of protected species (Anonymous 2007).

3.2 Side effects of legal protection on landowner attitudes

I found that the legal status of the flying squirrel has negatively affected forest owner attitudes towards the species. Although nearly all forest owners that responded to our survey were positive towards the idea of setting up nest boxes for a bird on their land, half would not like to set up nest boxes for flying squirrels (**II**). Thus, forest owner acceptance toward the same conservation action (setting up nest boxes) depends on whether the action is framed as flying squirrel conservation or not.

Although many citizens and politicians accept biodiversity conservation at the general level, its concrete and personal implications are less well tolerated (Schenk et al. 2007, Earl et al. 2010, Valkeapää and Karppinen 2013). Social conflicts generally begin in situations where the different parties cannot simultaneously achieve their goals (Bartos and Wehr 2002) either because of incompatible values or contested resources (Douglas and Verissimo 2013): e.g. when it is impossible for a landowner to sell timber and for conservationists to protect an old forest. In our survey, over 50% of forest owners said they would be worried about losing their freedom of making forest management decisions if their forest were occupied by flying squirrels, and nearly 40% said they would be worried about the economic consequences of having the species in their forest (**II**). However, the majority of forest owners with breeding sites and resting places in their forest estates were satisfied or somewhat satisfied with them and with authority actions in their case (**II**). In addition, forest owner attitudes toward having the species in their forest did not depend on whether they had nest sites in their forest, had experienced a visit by an environmental authority or had not experienced either (**II**).

If legal protection of the species has affected only a small proportion of forest owners (**I**), and restrictions have mostly been miniscule (**I**) and well tolerated (**II**), what then explains the high prevalence of negative attitudes? I found that i) attitudes toward the species in one's own forest and ii) policy-level attitudes concerning the conservation of the species loaded onto different factors (**II**). I also found that experience on the matter only affected policy-level attitudes – and that the claims of harming protected species were connected to this factor (**II**). It thus seems that forest owners use the flying squirrel as a symbol or synecdoche to represent and communicate their policy interests and agendas. The species appears to have become a symbol of broader socio-political disputes concerning private property rights, the power imbalance between rural and urban areas and the power of the EU. The case resembles the spotted owl case in USA (see Moore 1993). Perceived negative effects of species conservation should be understood as reactions to subjective, socially constructed realities – not only to objective conditions (Knight 2000, Herda-Rapp and Goedeke 2005, Douglas and Verissimo 2013). This means that objectively measurable consequences for forest owners may be irrelevant in solving the conflict.

Although it seems that in most cases, claims of forest owners destroying flying squirrel sites are just a part of the debate between stakeholders, the obvious conflict is not irrelevant for efforts to conserve the species. Social constructs are important because they shape the attitudes that influence individual behaviours (Bryman 2004). If hostilities intensify, emotions as opposed to facts tend to control debates (Wilson 1997), and the potential for destructive outcomes may increase (Douglas and Verissimo 2013). Protracted symbolic conflicts normalize the hostility between stakeholders, in which case the conflict may become symbolic in and of itself (Moore 1993). The problem is that certain organizations and professionals may benefit from, and therefore even encourage, social conflict over flagships species (Daniels and Walker 1995, Frazier 2005).

Various (but not necessarily mutually exclusive) solutions appear to exist for dealing with the flying squirrel conflict. Generally, efforts to protect forest biodiversity should not concentrate more on the symbol of habitat loss than the habitat itself (see Kouki et al. 2018). The flying squirrel does not appear to be a good flagship species in terms of promoting biodiversity friendly forestry for forest owners, thus conservation managers should try to find common ground elsewhere. The flying squirrel population can be conserved without ear tagging actions as flying squirrel conservation. Allowing forest felling at flying squirrel sites (e.g. in the form of continuous cover forestry) would be preferable in the sense that it would weaken the value of the species as a symbol of incompatible goals. However, if concrete actions to increase the quality of the forest matrix for the species are not taken, positive population-level effects should not be expected.

3.3 Predicting species occurrence

In study **III,** I modelled species occurrence with the detection/non-detection data of the national survey and available environmental datasets. Out of the tested environmental variables, average winter temperature had the largest predictive power for flying squirrel occurrence (**III**). Milder winters appear to explain why the species has been more abundant in southern and western areas than in the east or north (see Figure 6a), but I could not infer what mechanisms explain the effect of winter temperature. There are significant correlations between winter temperature and forest composition (e.g. area of agricultural land edges) and leaf-out and masting of deciduous trees that could determine e.g. food availability for the species (see e.g. Hoset et al. 2017). The results suggest that a rise in winter temperature may increase forest quality in central and northern areas, while potentially decreasing them in southwestern and coastal areas. The temperature cline has moved an average 186 km north-east in Finland between 1970–1989 and 2000–2012 because of global warming, and this has already been observed to cause bird species turnover (Virkkala and Lehikoinen 2017). Climate change has not been considered a major threat for the flying squirrel (Liukko et al. 2016, 2019), but it seems that the species monitoring programme should be used for testing whether the species abundance pattern is changing with moving temperature clines.

As expected based on species ecology, I found that the old forest habitat area had a positive effect on the species (**III**). According to Remm et al. (2017), an increase in the area of a >50-year-old spruce–deciduous forest in a 250-m radius has a positive effect until the area exceeded 40%, after which an increase in area decreases the occurrence probability of flying squirrels – which seems counterintuitive. However, 50–60-year-old stands may still lack tree cavities that are important resources for the species. Habitat heterogeneity may also be important for the flying squirrel, as various resources may be located in different habitat types (Mysterud and Ims 1998, Matthiopoulos et al. 2011). The positive effect of agricultural land edges on flying squirrel occurrence (**III**, see also Santageli et al. 2013a, Remm et al. 2017) also suggests that Finnish forests lack important resources for the species. Deciduous trees, providing food and nesting sites, may be more common and produce more catkins at edges (Hoset et al. 2017) because of the fertile soil and favourable microclimate. In North America, northern flying squirrels (Glaucomys sabrinus) seem to respond more to stand-level microclimate and food availability than to forest type or age (Wheatley et al. 2005).

I found support for the hypothesis that predation pressure could affect the regional abundance of flying squirrels: modelled predation pressure by Ural owls (*Strix uralensis*) correlated negatively with species' occurrence probability (**III**). Based on earlier studies Ural owls are known to locally affect flying squirrels, as flying squirrels are often absent from the close proximity of Ural owl nest sites (Byholm et al. 2012, Turkia et al. 2018). However, the Ural owl is not believed to play a major role in explaining flying squirrel density in the landscape (Selonen et al. 2010a, Selonen and Mäkeläinen 2017, Turkia et al. 2018). Our results imply that strong predation pressure may override the effect of habitat availability in southern Finland (**III**). An analogous situation has been observed with the northern flying squirrel (Forsman et al. 1984, Carey et al.

1992). A connection possibly exists between clear-felling -based forestry and predator pressure, as clear-felling creates favourable habitat for voles and thus affects the main food source of owls (Hakkarainen et al. 1996).

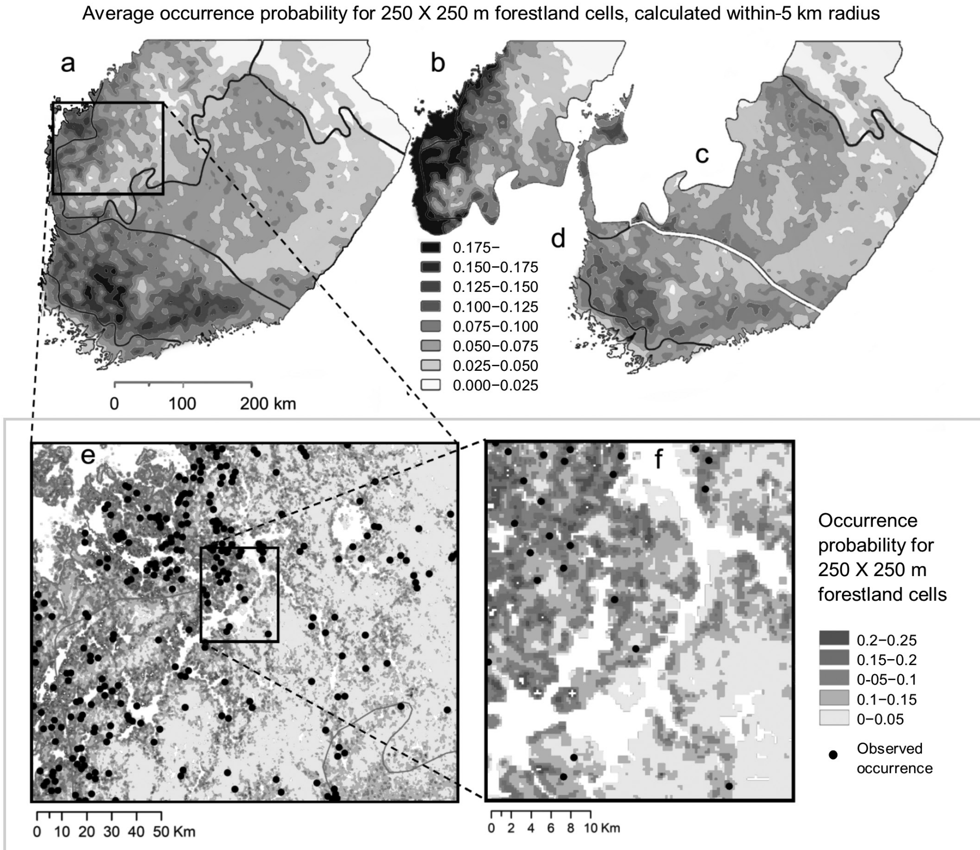

Fig. 6 Occurrence probabilities of a) the model for the whole study area, and b–d) of the three regional models, calculated as means for 250 x 250-m forestland cells within a 5-km radius in 2005. Panels e) and f) are examples of a full resolution map of the whole area model.

As breeding sites and resting places of the Habitats Directive are defined as sites that are, or have been, used by the species (Anonymous 2007), forest managers and operators need up-to-date information on nest sites – or at least information of which areas should be surveyed before forest felling. Although several environmental variables explain flying squirrel occurrence on some sites, the model's ability to predict the occurrence of specific sites and years remained poor or moderate (AUC 0.6–0.7, **III**). This is likely because available forest data do not include information on certain resources important for the species, and because of the survival and colonization dynamics of the species that create empty territories (Brommer et al. 2017). Projecting the model to the present day further increases the uncertainty of the predicted occurrence probability. As landscape-level factors also appear to play a major role in species abundance and site-level occurrence probability (**III**, Figure 6, Santageli et al. 2013a, Remm et al. 2017), the effectiveness of "precision strike conservation" of nest sites may be limited. It seems that we should pay more attention to forest policy targets (Haakana et al. 2017) and general forest management practices that affect habitats and resources important for the species. For example, we could increase the number of large deciduous trees and trees with cavities in all forest stands. The current practice is to leave old aspens as retention trees on clear-felling areas, but they likely die before the stand grows and thus a maturing forest may not provide nest sites for the species.

3.4 Evaluation of the monitoring programme

The conservation status of the flying squirrel has been defined from species monitoring data by interpreting the proportional decline in occupied survey plots as the proportional decline of population (see Liukko et al. 2016). Whether this interpretation is accurate depends on i) the selected sampling method (see Yoccoz et al. 2001, Pollock et al. 2002, McDonald 2004, Thompson 2012), ii) the abundance-occupancy-relationship (see Gaston et al. 2000, Joseph et al. 2006, Steenweg et al. 2018), iii) the detection probability and whether it remains constant or not (see Royle and Nichols 2003, Joseph et al. 2006) and iv) the scheme's power to detect true changes in population (Field et al. 2005, MacKenzie 2005, Rhodes et al. 2006, Ellis et al. 2014, 2015).

3.4.1 Sampling of monitoring sites

The monitoring effort needed for measuring the population trends of certain species depends, among other factors, on the size of the distribution area and spatial distribution of the animals. Monitoring of the Finnish flying squirrel population is challenging because the species' distribution area is large (over 150 000 km2) and population density varies at least spatially but possibly also temporally. To accurately measure the change in flying squirrel population, selected monitoring regions should be a representative sample of the species' distribution area, and selected monitoring plots a representative sample of the regions. Subjective selective sampling of monitoring sites was performed on two levels: i) selection of monitoring regions and ii) selection of survey plots in the monitoring regions. In addition, field workers could decide not to survey sites that they judged unsuitable for the species. The number of such sites has varied (see Table 1, p. 22). Generally, such subjective choices should be avoided, but they are not uncommon in monitoring schemes (see e.g. Andrén, Mönkkönen and Ovaskainen 2016).

Selection of monitoring regions and plots was based on prior information of species occurrence (Hanski 2006); while only approximately 10% of all survey plots were occupied during 2003–2005 (Hanski 2006, Santangeli et al. 2013a), the species was found from 28% of monitored sites in 2006. Observed occupancy may decline even if population size remains stable, if monitoring sites have higher than mean base-level occupancies. However, the high original occupancy on the monitoring sites may not indicate a severe problem for population monitoring if it is explained by stable quality differences between monitored and unmonitored sites. If the quality of monitored sides is permanently higher than the quality of unmonitored sites, the population should not e.g. grow in unmonitored sites if it is declining in monitored sites. Other sampling methods besides a random sample of the species distribution area are commonly used to increase cost-effectiveness or the power of trend detection. When monitoring resources are limited, attempting to exclude sites that are most likely unsuitable for the species both now and in the future is reasonable. The lower the occupancy of monitoring plots is, the more sites would have to be surveyed to gain a reliable estimate of population decline. In addition, if the goal of presence/absence monitoring is to detect population decays, focusing on high-quality habitat could be the optimal strategy (Rhodes et al. 2006).

However, such unequal probability sampling requires that factors affecting species occurrence probability are known and thus areas or sites may be stratified according to their similar quality (see McDonald 2004, Rhodes et al. 2006). Stratification was not done formally, but focusing on high-density areas and leaving out unsuitable or low-quality sites (e.g. pine-dominated forests) could have led to a somewhat equivalent sample. According to results of the species distribution model (**III**), monitoring has indeed focused on best-quality regions and sites (Figure 7a). However, when the occurrence on monitored and unmonitored sites is compared within the quality strata, occurrence on monitored sites is considerably higher than on unmonitored sites (Figure 8a). This could mean that the base-level occurrence on selected monitored sites was too high in relation to site quality. However, it is also very likely that actual quality differences that are missed by the distribution model exist between sites.

Another issue to consider is whether the relative quality of monitored and unmonitored plots changes over time. Mean temperature, area of agricultural land edges and soil fertility change very slowly, and the general patterns in regional spatial differences (Figure 7d) should therefore have remained more or less the same. On the other hand, the quality of growing forest stands changes much faster and clear-felling can change habitat area instantly. However, our comparison of the average area of >80-year-old habitat on monitored and unmonitored occupied and unoccupied survey plots in 2005 vs. 2015 does not indicate systematic major changes (Figure 8e and 9c–d). Monitoring data provide further proof for temporal consistency in regional quality differences: when the mean persistence of occupancy (Figure 10a) and colonization prevalence (Figure 10b) between two consecutive years are calculated from the monitoring data, differences between monitoring regions correlate with occupancy in 2006. This indicates that factors explaining the original occupancy still explain the current occupancy, and thus the relative differences in occupancy between various regions may have remained somewhat stable.

If selective sampling within monitoring regions (see Fig. 12) affects results, the observed occurrence would be expected to have declined faster in regions where the bias index (number of excluded survey plots/total number of survey plots) is the largest, i.e. there would be a negative relationship between bias index and the observed change in occurrence. However, the opposite seems to be true: observed occurrence has declined fastest in areas with smaller sampling bias (Fig. 11 a–e). Observed occurrence has even increased in regions with a small bias index when calculated from year 2008 or 2009 (see also Fig.12). During these years, field workers considered over 300 sites uninhabitable (see Table 1) and therefore did not survey them. If these sites are later surveyed, it could lead to an increase in observed occurrences, but still should not explain the positive relationship between bias index and change in observed occurrence.

The positive relationship appears to imply that some other factor is affecting the opposite direction than the potential effect of selective sampling within the monitoring regions. Although an ecological explanation may exist for this pattern (e.g. climate change may favour the species in northern areas, **III**, see Fig. 12), it could also be caused by the selection of monitoring regions. As the original survey sampled approximately 1% (or even less) of forestland, a high level of stochasticity is expected in the observed occurrence: in certain regions observed occurrence in the survey sites could have been much lower or higher than the true occurrence in that region (see also **IV**). As regions where observed occurrence was high were favoured, the subjective selection of regions could unintentionally have favoured regions were the base level for occurrence (observed occurrence on monitoring plots) was higher than the true occurrence in that region. Such a bias may lead to a decline in observed occurrences in regions where the base level of the observed occurrence was highest – and to an observed relationship between bias index and change in occurrence because of the relationship between bias index and original occurrence (Fig. 11 f).

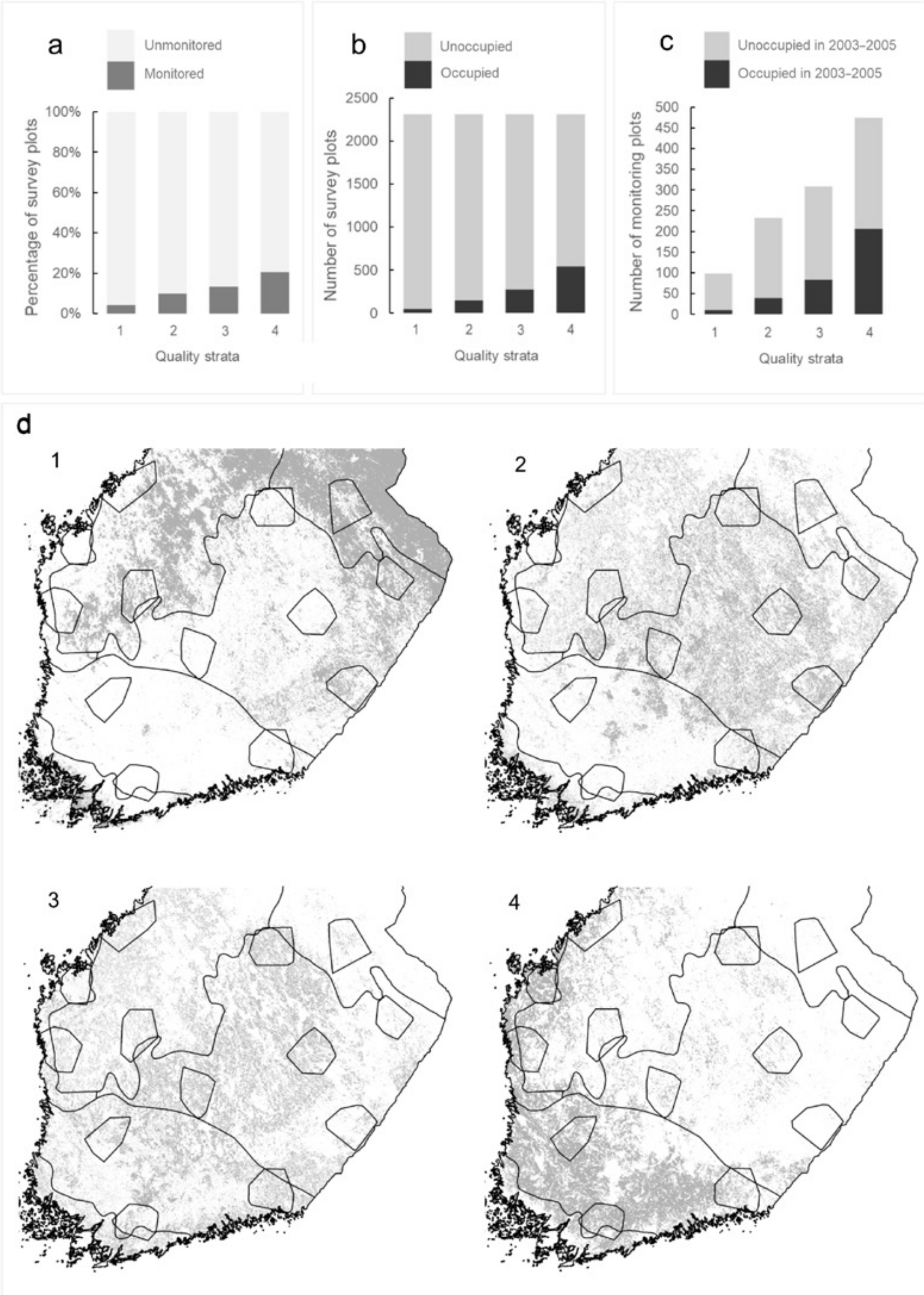

Fig. 7 a) Distribution of monitored survey plots on different-quality sites defined by species distribution modelling (SDM) for 2005. b) Number of originally occupied sites on different-quality sites defined by SDM for 2005. c) Number of occupied and unoccupied monitoring plots in different strata. d) spatial distribution of different-quality areas. Black polygons show monitoring regions. Quality strata 1 includes the worst 25% of all survey sites; quality strata 4 includes the best 25% of all survey sites.

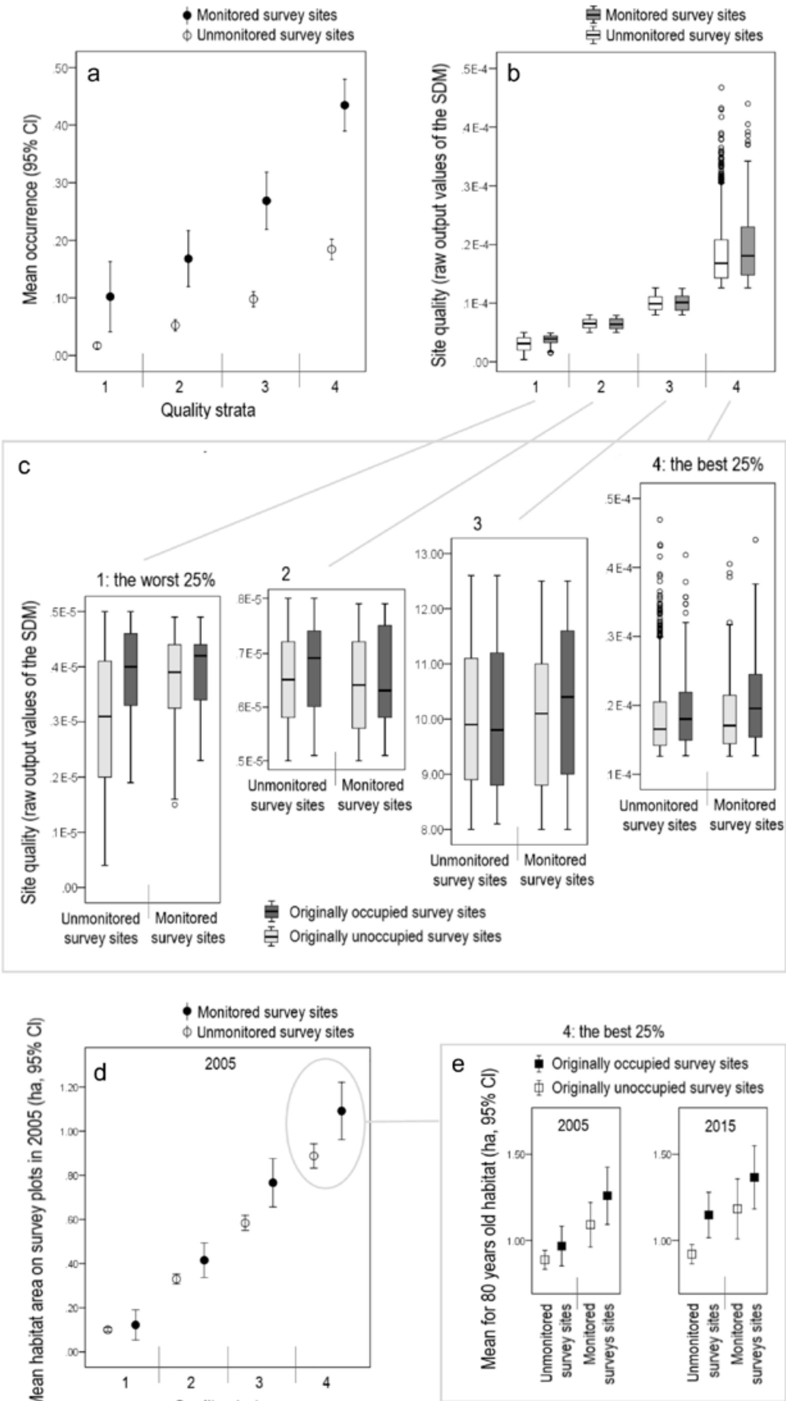

Fig. 8 a) Species occurrence in monitored and unmonitored survey sites during 2003–2005 within the quality strata. b) site quality of monitored and unmonitored sites within the quality strata. c) site quality of occupied and unoccupied plots that were unmonitored vs. monitored. d) area of >80-year-old habitat on monitored and unmonitored plots in 2005. e) area of > 80-year-old habitat on occupied and unoccupied sites in 2005 and 2015. Calculation is based on forest inventory datasets with various resolutions and may therefore not be fully comparable.

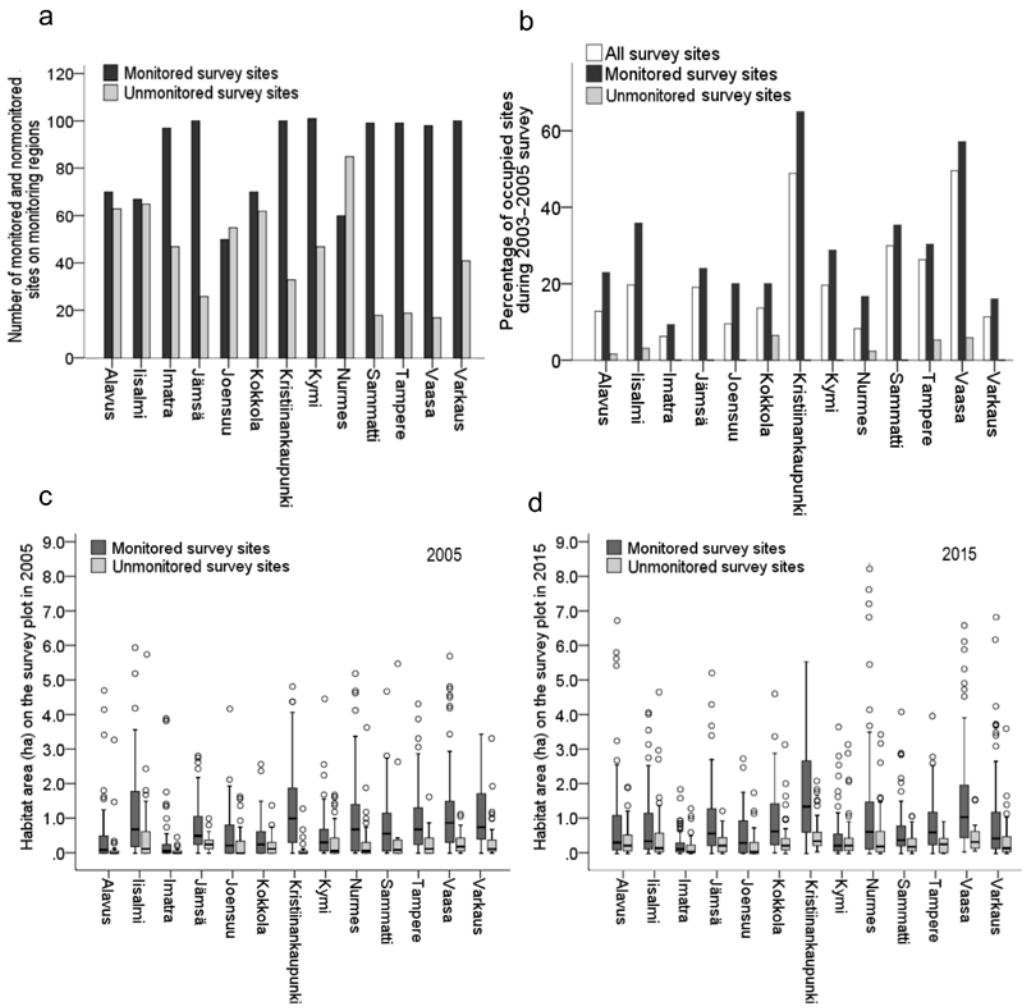

Fig. 9 Comparison between monitored and unmonitored survey plots in the monitoring regions: a) total number of monitored and unmonitored survey plots within the monitoring regions (defined as 100% convex minimum polygons), b) occupancy in regions during 2003–2005, c) habitat area in survey plots in 2005 and d) 2015 (areas are not fully comparable between the years).

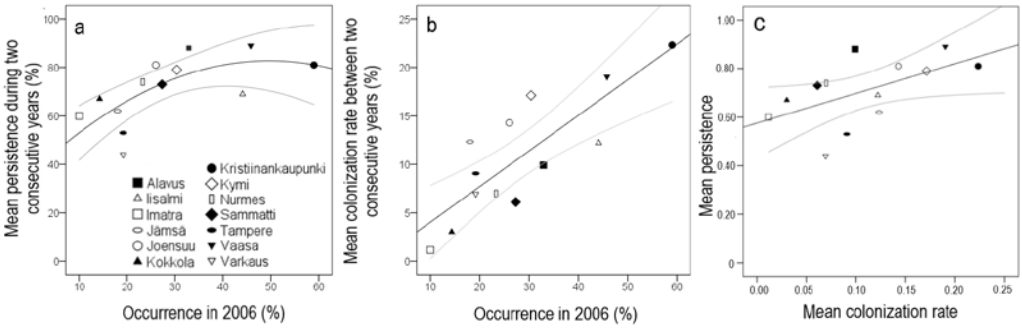

Fig. 10 Regional effect on species occurrence: a) mean persistence of occurrence on monitored survey plots in different monitoring regions between two consecutive years (during 2005–2017), b) mean colonization rate between two consecutive years, c) relationship between persistence and colonization rate.

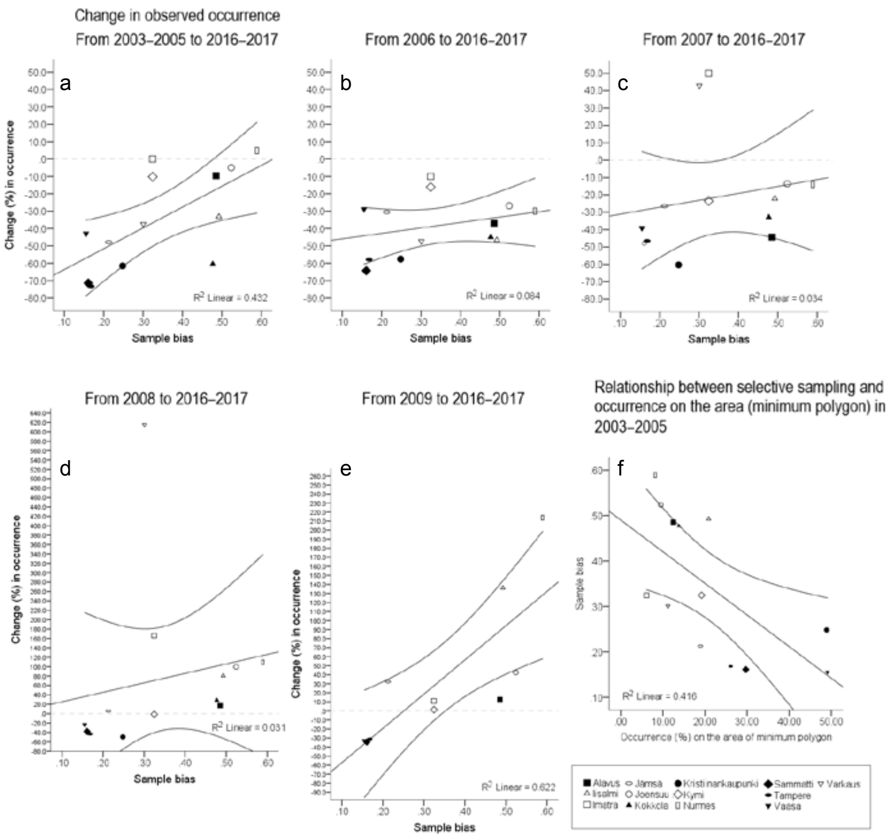

Fig. 11 a–e) Relationship between selective sampling of survey plots within monitoring regions and observed change in flying squirrel occurrence. f) Relationship between selective sampling of survey plots within monitoring regions and observed occurrence in 2003–2005 on all survey plots.

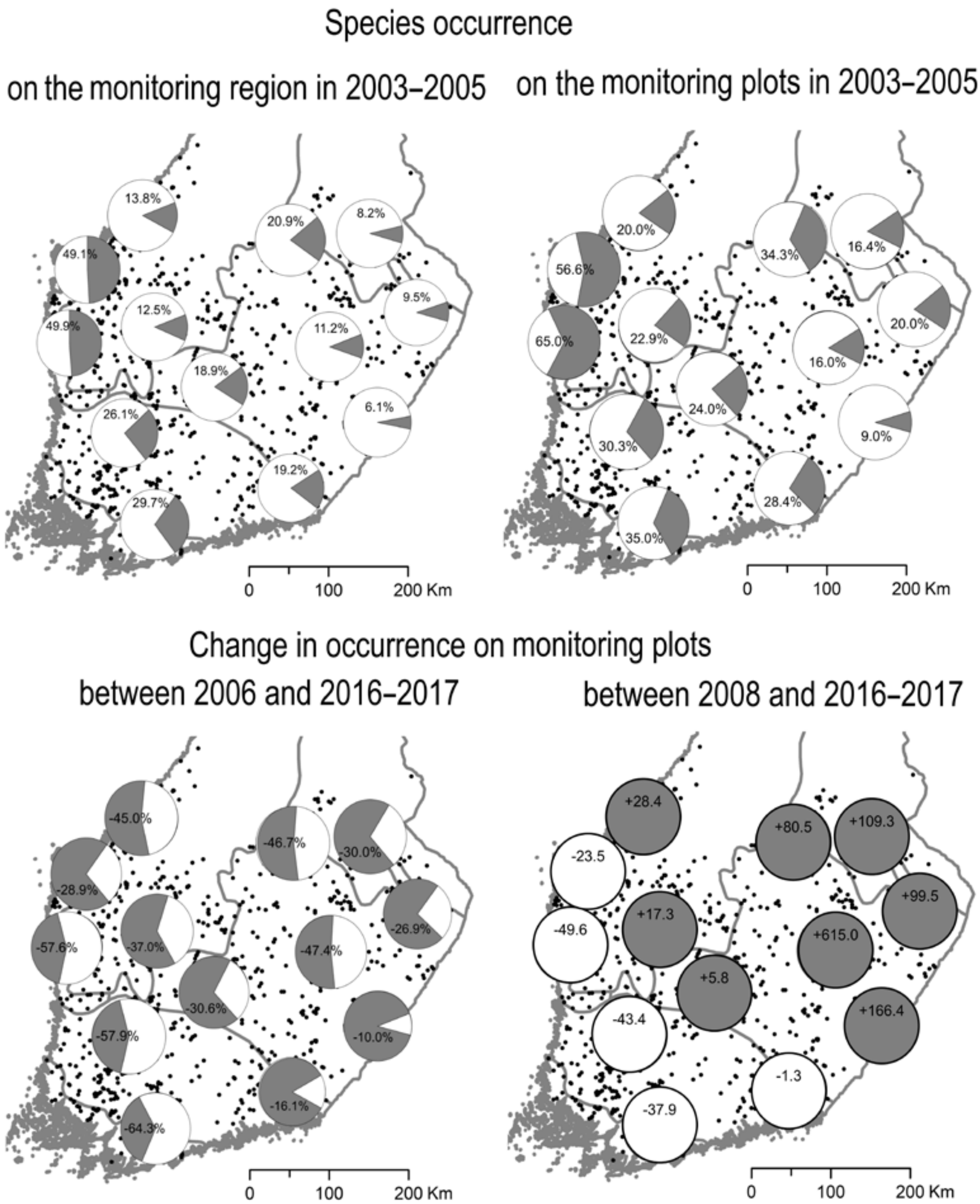

Fig. 12 Species occurrence on the monitoring regions and monitored sites during 2003–2005 and observed changes in occurrences. Note the spatial pattern in the observed change in occurrence between 2008 and 2016–2017. Proportionally large increases in the eastern and northern monitoring regions are results of small differences in absolute numbers of occupied sites.

3.4.2 Relationship between observed occupancy and abundance

The proportional change in female and male numbers (species sex-ratio is even; Selonen et al. 2010b) is assumed to correspond to the proportional change in occupancy at the monitoring sites (Rassi et al. 2010, Liukko et al. 2016). This would be true if an occupied site corresponded to one adult female (Hanski 2008). Sites found to be occupied are believed to mostly be female nest sites and territories, because males also spend most of their time on these sites during winters and springs (Hanski 2008). Although males can use many forest stand types when moving around in their home ranges, they often move rapidly between core areas (Selonen and Hanski 2003, Hanski 2008). Accumulation of faeces likely depends on the number of animals and on how much of their time they spend on a given plot. A small number of pellets makes discovery more unlikely. Also, young forest patches have not been screened for pellets (Hanski 2008), and therefore these movement habitats were not classified as occupied. Nevertheless, it seems plausible that sometimes males are observable outside female territories. Also, more than one female can use the same monitoring plot (see Figure 13). According to mark-recapture data from Vaasa, the mean distance between neighbouring female nest boxes has been 340 m (SD 210 m, n=153, data from Selonen and Wistbacka 2017). If a decrease in population size leads to an increase in the mean distance between females, the population could decrease more rapidly than the observed occupancy decreases. This possibility has been suggested by Sulkava et al. (2008), who tested a survey method used by the monitoring scheme with an ear-tagged study population. Results of this study suggest that the method results in increasingly upward-biased population size estimates for a declining population (Sulkava et al., 2008).

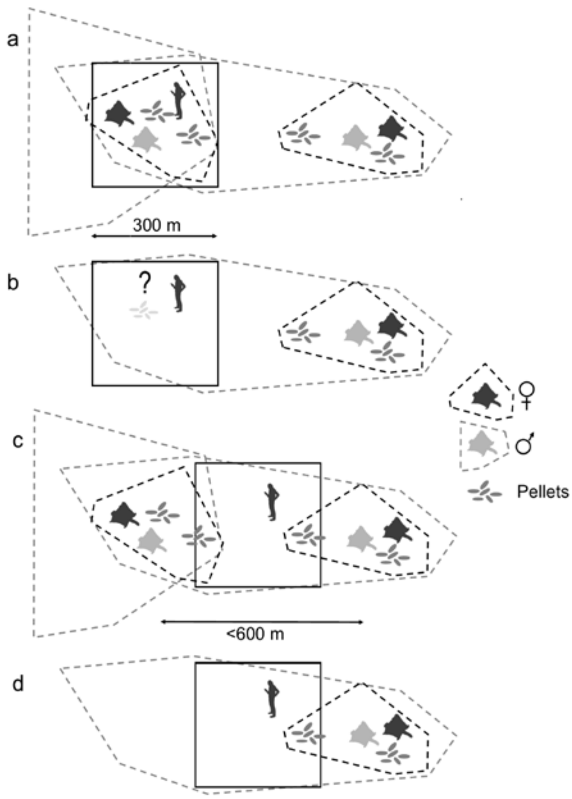

Fig. 13

Schematic representation of a possible relationship between observed occurrence and number of individuals. The monitoring method is based on information of species spatial behaviour. Our presumption is that survey plots observed to be occupied are in most cases occupied by one female (a) and males are unobservable outside female territories (b). Thus, the relationship between a decrease or increase in female numbers and a decrease in observed occurrence is linear. However, more than one female and male can use the same monitoring plot if the density of females is high enough (c), and disappearance (d) or colonization may not be detected. In fact, individuals may not even be on the monitoring plot.

Using simulated populations, we found that the detectability of flying squirrel males outside female territories may have led to a significant underestimation of population decline, at least in certain regions (**IV**). Even if males are only located in female core areas, the population may have declined more than the observed occurrence in the monitoring regions suggests. When comparing predicted mean population sizes on four monitoring regions in Western Finland, a -46.7% decline in occurrence observed between 2006 and 2017–2018 corresponds to a -57.5% or -52.6% population decline if males were observed outside female territories or if individuals were observable only on female territories, respectively (Figure 14, **IV**). Thus, the criticism by Sulkava et al. (2008) over using proportional change in occurrence as an accurate measure for population decline (Liukko et al. 2016) seems justified. However, the bias on average increases when the initial occupancy is larger. This may imply that the risk of underestimating population decline may be lower in areas where the base level for population density had been or is now lower than it was in western Finland in 2006. We did not manage to obtain realistic populations in low-density monitoring regions, and thus we were unable to estimate how large the difference may be in northern and eastern parts of the distribution area. We should also note that the virtually derived occupancy-abundance- relationship rests on several assumptions. Empirical data on the distribution and observability of pellets in relation to individuals and their home ranges are needed for assuring these results. At the moment, we do not really know how the spatial distribution of actual individuals changes in declining natural populations, e.g. do individuals in low-density areas have problems finding mates, as simulated individuals did (**IV**). Demographic stochasticity and/or the Allee effect (Stephens et al. 1999, Gascoigne et al. 2009) may, in theory, have a significant effect on low-density flying squirrel populations.

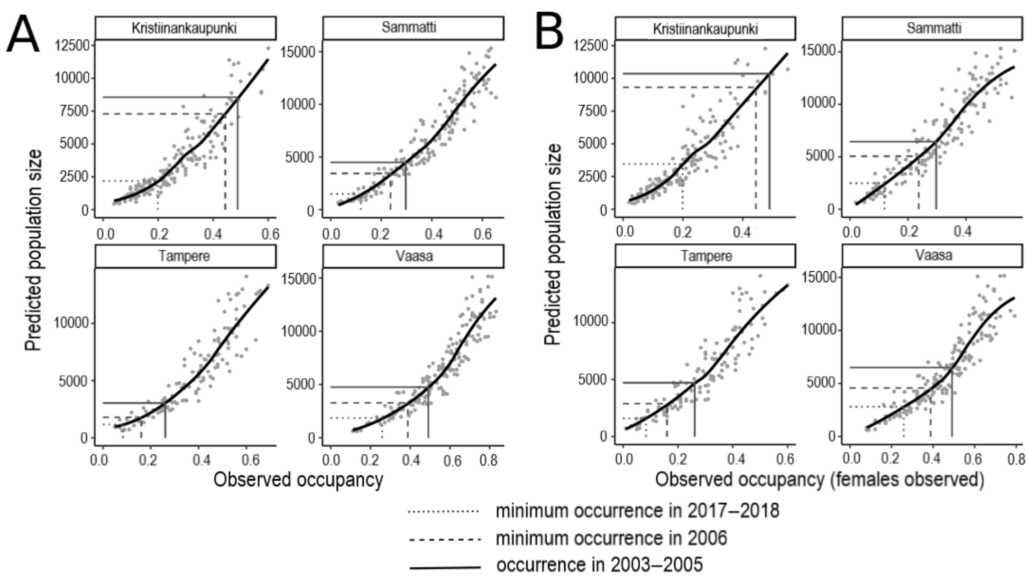

Fig. 14 Regional occupancy-abundance relationships. Panel A illustrates the relationship between simulated occupancy level and simulated population size, for different occupancy levels of interest (2006 and 2017–2018), and panel B illustrates the same under the assumption that only female core areas are observed.

3.4.3 Power

The lack of power for detecting population trends (Type II or β error) is a common problem of presence/absence monitoring schemes – a power analysis should therefore be undertaken to ensure that schemes can actually achieve their goals (Rhodes et al. 2006, Ellis et al. 2014, Ramsey et al. 2015). However, the selective sampling method may increase the risk of Type I (α) error: identifying a trend (in this case: a negative trend) when no trend exists. Power analysis cannot be conducted reliably if the sample is not drawn by random sampling. As the occurrence on monitored sites declined drastically during 2006–2009, the risk of Type I error is presumably reasonably small if only data collected after 2009 are used. There were a total of 158 occupied plots in the monitoring regions in 2018. This should be enough for detecting significant and systematic population trends in the monitoring regions if the monitoring scheme is continued, but the proportional change in occurrence should not be considered an accurate estimate of population change. A much more rigorous scheme is needed to formulate an accurate estimate (see e.g. Ganey et al. 2004)

3.4.4 Accuracy of reported population trend

My original goal was to infer the proportional change in the size of the Finnish flying squirrel population from the monitoring data. But the results of study **IV** are applicable only for monitoring data that are unbiased. If the proportional change in observed occurrence is biased, the resulting estimate for proportional change in population will also be biased. As I was unable to estimate the potential effect of the selective sampling, the scientific quality of such calculations would be low.

The critique (Sulkava et al. 2008) concerning the population size estimate of 143 000 females (Hanski 2006) proposes that the method used for calculating the population size may overestimate female numbers. The reason for this is that some proportion of occupied survey plots may either have only a male home range or may contain only part of a female territory (see Fig. 13). This means that individuals that are actually outside the plot are “observed” on the plot.

3.4.5 Why, whether and how to monitor the flying squirrel population?

Defining a realistic goal/goals for monitoring is the first step in planning a successful monitoring scheme. Available resources often set the limits for what kind of changes are detectable. The annual budget of the flying squirrel monitoring was 60 000 euros in 2017 (J. Valkama personal comm.). Population monitoring was initiated because of concerns over the negative population trend (Hanski et al. 2001) and because the Habitats Directive requires member states to monitor and report the conservation status of individual habitats and species listed under the Directive Annexes every six years (92/43/EEC, Article 11, 92/43/EEC, Article 17). Thus, the primary goal of monitoring has been to fulfil the requirements of the Habitats Directive: provide information that can be used for reporting and ensure that the “favourable conservation status” (see Epstein 2016, Epstein et al. 2016) is achieved, or that a population is recovering with the measures taken. Monitoring is, therefore, focused on detecting whether the population is in ongoing decline and/or whether the natural range of the species is shrinking, but the data are also used as a measure of population decline speed (Liukko et al. 2016, 2019). These are typical goals for long-term mandated monitoring programmes (Lindenmayer and Likens 2009, 2010a), as documenting and communicating negative trends has been at the core of conservation science (see e.g. Ripple et al. 2017). However, pure surveillance monitoring may be an ineffective use of limited conservation resources.

Although monitoring schemes may have benefits that are not directly linked to the production of new ecological information, e.g. schemes may encourage wanted actions among the public and policymakers (Tulloch et al. 2013), the lack of information concerning the decline in biodiversity may not be the primary barrier to the public support for actions (Masuda and Scharks 2018). Thus, effective monitoring does not only demonstrate a decline or its reasons, but also provides crucial information needed in the conservation process; e.g. it tests the hypothesis for the most effective management methods (Nichols and Williams 2006). The general focus of species monitoring programmes has recently begun shifting from producing coarse-level information on population trends towards increasing general scientific knowledge and understanding the effects of certain intervention or management activities. As the goal of the Habitats Directive is on maintaining and/or restoring a favourable conservation status for species of community interest, mere surveillance monitoring is not an adequate solution in the case of declining populations: monitoring should be connected to adaptive conservation policy and practices. As the former population decline estimates reported in the Finnish Red Data Books (Rassi et al. 2010, Liukko et al. 2016) have not triggered conservation actions or change in forest management, a direct relationship does not appear to exist between population monitoring and species conservation. Increasing the relevancy of population monitoring for policy and management would require setting good questions that test real policy and resource management options. For this, we need a collaborative partnership between policymakers, managers, conservation scientists and statisticians (Lindenmayer and Likens 2010b). Generally, conceptual models of the systems help in framing good questions for monitoring schemes (Lindenmayer and Likens 2010a, 2010b). Therefore, I made a tentative conceptual model for a flying squirrel monitoring scheme (Figure 15). However, it is possible for various parties funding monitoring schemes and using the collected data to have different, even conflicting goals. For example, a reported negative population trend can be used to justify forest conservation and conservation legislation in general. On the other hand, information collection may be used to justify a delay in actions (Nichols and Williams 2006) or just for the sake of reporting. The accuracy of an estimated population decline, or ecological information on the reasons for the decline would not be that crucial for either of these goals. Thus, even if researches were to believe that the accurate detection of a population trend and the production of new ecological information were among the most important quality traits for all monitoring schemes, these may not be as important for all stakeholders. Monitoring resources appear to be granted and spent mostly on data collection, and less consideration is given to data analysis, interpretation and reporting (Caughlan and Oakley 2001, Lindenmayer and Likens 2009). This is a common problem for all types of monitoring programmes (Caughlan and Oakley 2001, Lindenmayer and Likens 2009).

If the accuracy of the population trend estimate is considered important, the results of this thesis should be used for developing the monitoring scheme. Because of the used methods, especially the way the monitoring regions were selected and defined, it is not possible to infer reliable change in species' occurrence in Finland since the 2003–2005 survey. The reported estimates (Rassi et al. 2010, Liukko et al. 2016, 2019) are highly uncertain because the base level used for occurrence, calculated from the first years of monitoring, may be biased. Producing a more reliable estimate for the change in occurrence requires forming a new sample from the original 2003–2005 survey plots. Unbiased data are also needed for modelling and explaining changes in occurrence. If complete resampling is not an option, partial resampling may allow estimating the magnitude of the effect of selective sampling (see Figure 16).

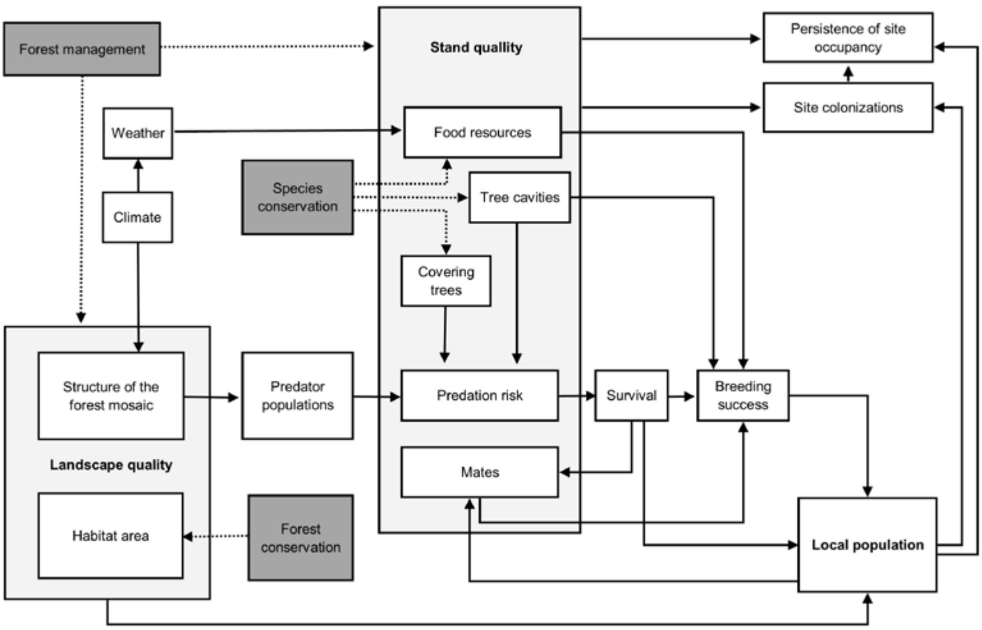

Fig. 15 Conceptual model.

Fig. 16
The map shows the most favourable areas for the species according to a projection of the SDM (III, light grey areas) and current monitoring regions (white polygons). The forest vegetation zone of southwestern Finland is under-monitored in relation to its predicted quality for the species.

Above all, monitoring should not be conducted only for the sake of trend reporting. Reliable population monitoring and species-by-species conservation status estimations are resource and time consuming. An ecosystem-level threat assessment is suggested as an alternative approach (Rodríguez et al. 2011). In Finland, the conservation status of habitat types is assessed using the international IUCN Red List of Ecosystems method (IUCN 2015, Keith et al. 2013). The main habitats of the flying squirrel are classified either as Endangered (Old conifer-dominated herb-rich heath forests and mesic heath forests), Vulnerable (Mature conifer-dominated mesic heath forests) or Near Threatened (Mature conifer-dominated herb-rich heath forests) (Kouki et al. 2018). Population monitoring should provide truly additional information that can be used for species conservation – otherwise it remains political or academic replacement behaviour (Whitten, Holmes and MacKinnon 2001). The monitoring scheme should be based on 1) good questions and 2) rigorous study methods. In addition, 3) data collection should be coupled with subsequent statistical analyses of the monitoring and environmental data (Haakana et al. 2017) – including information on opportunistic manipulations due to forest management (Lindenmayer and Likens 2010a, 2010b). Because of the methodological and other issues in effectiveness, I would recommend developing the scheme using an adaptive monitoring framework (Lindenmayer and Likens 2009, 2010b). Collected data should be readily accessible to researchers both for peer-review and use.

3.5 Does usability, relevance or scientific quality of information make a difference?

Conservation scientists are met with a growing demand to produce information on effective conservation and management actions (see e.g. conservationevidence.com). Monitoring and evaluation are crucial tools in ensuring that we are not wasting conservation resources, but as monitoring also consumes resources, the same requirement of effectiveness should apply to research. Although no one doubts that high-quality information can lead to better decisions, this may not happen, as policy actors seldom use information as a direct input to their decisions (see Bauler 2012) – regardless of the apparent relevance of the information. This means that we should start by assessing whether we can already make adequately informed decisions without further research (Pullin et al. 2013). In many cases, lack of political will and resources may be the actual problem – not the lack of information (Rose et al. 2018). Thus, defining research questions is a crucial step for conservation researchers: the framing of questions should be relevant to both researchers and users of knowledge to increase the flow between knowledge and action (Cook et al. 2013, Montambault 2015). The problem is, researchers may be detached from the practical reality of conservation and information needs. Separation of conservation research and practice can make it difficult for researchers e.g. to acknowledge crucial economic and societal constraints. Because of this, researchers may not study ‘real world’ questions of management relevance (Knight 2008, Arlettaz 2010, Lindenmayer and Likens 2010a, 2010b). Generating science that will effectively inform management decisions requires that the production of information is relevant and timely; authoritative, believable and trusted; and developed via a process that considers the values and perspectives of all relevant stakeholders (Cook et al. 2013). Effective information and knowledge transfer thus requires strong partnerships between scientists, policymakers and managers.

Quantifying the impact and relevance of scientific research may be difficult (Sutherland et al. 2011), and few researchers assess and report the policy impact of their work (Ritter and Lancaster 2013). As it happens, the first article of this thesis (**I**) hit a policy window (see Rose et al. 2017): it was published at the time when the future of the preventative prior approval procedure for breeding sites and resting places and revision of the guidelines for the sites were under consideration. I had also written a more accessible report on study **I** that was targeted to Finnish authorities (Jokinen 2012). In addition, another independent study published in a scientific journal examining breeding sites and resting places was available (Santangeli et al. 2013b). So, it is possible to examine whether and how decision-makers and other stakeholders cited these studies and the information provided for them in grey literature.

Out of the three available papers, the report (Jokinen 2012) seems to be the most cited in the context of species conservation in Finland; e.g. the new guidance material cites the report (Anonymous 2016). The main differences between the report and scholarly articles was that the report was published in an open-access series of the Finnish Environmental Institute (SYKE), it was in Finnish, described the practice in detail (including images) and was written more from a practical than a scientific perspective. The report is likely easier to find and otherwise more accessible and usable than the scholarly papers. As scientific journals target international audiences, articles may not contain information in a form that would be relevant and salient for local stakeholders. Generally, scientific papers are not the most widely used information sources for decision-makers and managers (Pullin et al. 2004). The report being published by SYKE may also have made it more legitimate or credible in the eyes of certain readers compared to scholarly papers published by commonly less-known international journals. Out of the two articles, the paper by Santangeli et al. (2013b) has drawn more scholar citations than study **I**, but study **I** is more often cited by national grey literature and in the context of decision-making. The two scholarly articles had somewhat different research questions. In study **I**, I considered the effectiveness of the conservation measure at the scale of the Finnish flying squirrel population and explained species persistence by the quantity of remaining habitat. Santangeli et al. (2013b) focused only on breeding sites and resting places they had examined and on proving that used guidelines for forest management are inadequate for the species.

More interesting than the number of times different papers have been cited, is which information was cited, in what context and what impact it may have had on policy. My calculations on the total effectiveness of breeding sites and resting places (Jokinen 2012, **I**) was used partial reasoning behind the changes made to the Nature Conservation Act; namely removing the legal obligation for regional environmental agencies to make authority decisions on forest management (Anonymous 2015a). Deregulation seems to be connected to the government's general plans of "reducing the net number of regulations and increasing the use of alternative instruments" to decrease the administrative burden (Anonymous 2015b). The prior approval procedure burdened environmental authorities more than expected: protection of the flying squirrel took up to one fifth of all species protection resources allocated by the ELY Centres (Kemppainen and Anttila 2011). By 2012, environmental authorities had made ca. 2000 decisions concerning potential breeding sites and resting places of the Siberian flying squirrel (Miettinen 2012, Jokinen 2012). The government had also expressed that "no further national regulatory measures will be taken in connection with the implementation of EU regulations" (Anonymous 2015b). So, it seems that information was used for justifying pre-existing preferences for decisions and actions (see Weiss et al. 2005), not as a base for them. Information seemed to have more political and symbolical value than instrumental value for policymakers: if increasing the effectiveness of species conservation had been a main goal, the ecologically ineffective procedure would have been replaced with more effective measures (Vuorinen 2017).

Conservationists and researchers have felt justified distrust in the ecological adequacy of the first ministry guidelines for safeguarding nest sites (Anonymous 2004). Information on species habitat requirements was available at the time (see Hanski et al. 2001) and therefore a lack of ecological information was not the reason for the disparity between species' home range requirements and guidelines for safeguarding nest sites. The original guidance document stated that guidelines for breeding sites and resting places would be updated according to information from future studies (Anonymous 2004), but no effort was made to implement adaptive management or e.g. to use the species' monitoring scheme for this purpose. Furthermore, the renewed guidelines do not require application of any additional measures (Anonymous 2016) although studies have shown guidelines to not safeguard ecological functionality of the nest sites.

Another interesting example of information use comes from how the population trend and size estimates are used. The population estimate of 143 000 females (Hanski 2006) is claimed to be highly inaccurate (Sulkava et al. 2008), yet this number has become enshrined in the grey literature (e.g. Anonymous 2015a). Likewise, critique towards the inferred proportional population decline (Sulkava et al. 2008) was ignored in former conservation status assessments (Rassi et al. 2010, Liukko et al. 2016). The recent assessment acknowledges that the population may decline faster that species' occurrence, but does not consider the possible effect of selective sampling (Liukko et al. 2019). Generally, persons filter information in a way that makes sense according to their social group (Nickerson 1998, Kahan 2010, Kareiva and Marvier 2018), and are more likely to accept and use information that aligns with what a person (perhaps unconsciously) wants to hear. Because conservation science is a goal/mission-oriented science, it is also prone to such confirmation bias. Errors in line with "conservationists' dogma" may remain undiscovered (Kareiva and Marvier 2018).

4. CONCLUSIONS

In this thesis, I found that the lack of occurrence information leads to a high risk of accidental destruction of flying squirrel nest sites and thus limits the effectiveness of legal protection (**I**). The case demonstrates why the effect of an intervention should be monitored and assessed in the area where it is expected to have an effect along with the effective scale (Pullin et al. 2013). In study **III,** I provided an occurrence probability map for southern and central Finland. However, as the ban on deterioration or destruction of breeding sites and resting places only applies to sites that are or have been occupied by protected species (see Anonymous 2007), increasing the effectiveness of flying squirrel conservation with the current strategy would require regular surveys over large areas. The obvious impossibility of upholding sufficiently comprehensive and updated fine-scale information on nest sites means that additional measures are needed to achieve a favourable conservation status. The used measures should correspond to the scale of the problem: decrease and deterioration of the species main habitats (Haakana et al. 2017) to affect the species conservation status in Finland.

The evidence base for species-focused protection laws is generally weak. Lack of compliance, pre-emptive destruction and poor administrative targeting may reduce the effectiveness of legal protection (Barret et al. 2013). Species distribution models indicate that large-scale factors affect the regional abundance of the flying squirrel (**III**), and regional abundance affects the occurrence probability on a specific site (Santangeli et al. 2013a). Therefore, general forest management practices affecting important resources on the scale of local populations may play a key role for the population trend. When considering the currently predominant clear-felling-based forest management methods, we could maintain or increase the area suitable for the species by increasing the area of protected forests and by widening the time window that flying squirrels can exist in commercial forest stands. The latter could be implemented in four general ways: we could i) postpone the time of final cut of a forest occupied by the species, ii) increase the proportion of mature stands suitable for the species by growing forests with suitable tree species compositions and important resources, and/or iii) make potential stands usable for the species earlier. Options ii) and iii) would likely be socially and politically the most palatable, as they do not require compensations for forest owners or detailed up-to-date information of occurrence and fine-scale spatial planning – only coherent forest policy and management ensuring that resources important for the species are or will be available at the correct time. However, these options would require setting concrete and measurable objectives for improving the quality of the forest matrix; simple recommendation for good forest management may not be enough for achieving significant changes in forest landscapes.

Legislative protection affects by changing human behaviour towards the subject of protection. Thus, we may need to use multidisciplinary approaches to develop our understanding of the effects of conservation policies. Although attitudes toward flying squirrel conservation are not determined by direct costs imposed on forest owners, the species' legal status has made it a conflict organism in Finland (**II**). Therefore, it is not an optimal flagship species in terms of promoting biodiversity friendly forest management to forest owners. Improving general forest management would not create disincentives that could motivate some forest owners to harm flying squirrel nest sites.

The basic ecology of the flying squirrel is well-studied in Finland, but questions connected directly to conservation policy and management have received much less attention. In some cases, existing data are not used, analysed or synthetized, or results have not been provided in the most usable form to benefit decision-making and management. For example, results of existing species distribution models have not been presented as occurrence probability maps that could be used for targeting surveys or developing monitoring and conservation efforts at the national level (but see Jokinen, A. 2010). Shortcomings of research and monitoring may, in the worst case, lead to misleading conclusions. For example, studies evaluating the impact of safeguarding breeding sites and resting places have not evaluated the effectiveness of this conservation strategy in relation to the scale of the problem it seeks to address.

I also found that the species' monitoring scheme has used a sampling method that may lead to an error when the magnitude of population change is estimated from the data (**IV**). In addition, the used sampling can decrease the value of the collected data in modelling and in explaining changes in species occurrence. The scheme has focused on data collection, while programme development, data management and analysis, interpretation, and reporting have achieved less attention. Methodological problems and focusing too much on data collection are common problems of monitoring programmes (Caughlan and Oakley 2001, Lindenmayer and Likens 2009, 2010b). It seems that flying squirrel monitoring has been driven more by a political directive than by carefully posed questions and objectives. The scheme has not been integrated into the decision-making process, and there seems to not be a threshold for decline in occurrence that would lead to a change in management actions. Nor has the scheme produced information that can be used for selecting the best management actions. The scheme could have been used for developing adaptive management, but this opportunity has not been used. Funding the mere documentation of occurrence decline seems more of a replacement activity or delaying tactic than a justified use of conservation resources (Whitten, Holmes and MacKinnon 2001, Nichols and Williams 2006). Generally, monitoring schemes should be more often used to evaluate the efficiency of management policies and alternative actions (Nichols and Williams 2006). However, this may complicate designing the schemes, as dialog between researchers, managers and other stakeholders is needed to select ‘real world’ questions of management relevance. Opening the monitoring data to the research community would widen the expertise and thus lead to new findings, methodological improvements and increase the reliability and effectiveness of the scheme.

Although in this thesis I have focused on filling in gaps that basic research has left uncovered, I recognize that there are limits to the effectiveness of the evidence-based clinical approach for conservation (Mermet et al. 2013). Whether a discovery has an impact is not solely dependent on the quality or relevance of the underlying science (Sutherland et al. 2011). The case of the flying squirrel supports the general observation that conservation research provides direction to policy, and research findings lead to action, mostly in practice-related decision contexts with a high degree of technicality and when societal and political impacts are small (see Bauler 2012). When societal and/or political impacts are thought to be significant, decisions are compromises between various goals. In such cases, research is used to support or justify pre-existing preferences or actions, and thus new information may only have a legitimizing function (Weiss et al. 2005, Nichols and Williams 2006). In the case of the flying squirrel, the main problem for conservation effectiveness is apparently not a lack of information on species ecological requirements, but conflicting goals for forest management and lack of political will and resources for making ecologically effective actions. In Finland, the flying squirrel is apparently conserved more in the letter than in the spirit of the Habitats Directive. Limited conservation resources were wasted on the previous ineffective approval system that seemed to have been enacted mainly to protect forest owners and felling actors from legal consequences – not so much to safeguard the ecological functionality of flying squirrel nest sites. The population monitoring scheme has not been integrated into the decision-making process or conservation practice, and therefore reports of a steep population decline (Rassi et al. 2010, Liukko et al. 2016) have had no impact on species’ conservation. Perhaps conservation researchers should “choose their battles” more wisely. Generally, further research is needed, and effectiveness of conservation actions should be monitored and evaluated when the best management option is not clear, and resources and the will to apply adaptive management are available (McDonald-Madden et al. 2010).

To conclude, research and management should be considered two sides of the same coin; “neither exercise makes proper sense unless accompanied by the other” (Pullin et al. 2013). This requires creating much stronger, true partnerships between policymakers, managers and researchers of various disciplines.

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